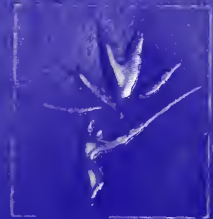


Bothalia

A JOURNAL OF BOTANICAL RESEARCH

Vol. 27,1

May 1997



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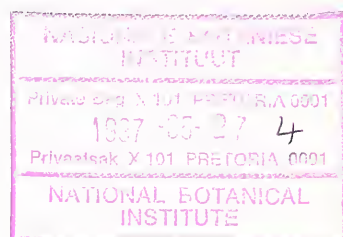
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Scientific Editor: O.A. Leistner
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ISSN 0006 8241

May 1997

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Notes on *Plectranthus* (Lamiaceae) from southern Africa

E.J. VAN JAARSVELD* and T.J. EDWARDS**

Keywords: comb. nov., Lamiaceae, *Plectranthus* spp., southern Africa, spp. nov., stat. nov., taxonomy

ABSTRACT

Four new *Plectranthus* taxa from South Africa are described: *P. malvinus* Van Jaarsv. & T.J.Edwards, *P. saccatus* subsp. *pondoensis* Van Jaarsv. & S.Milstein, *P. purpuratus* subsp. *tongaensis* Van Jaarsv. & T.J.Edwards and *P. purpuratus* subsp. *montanus* Van Jaarsv. & T.J.Edwards. *P. aliciae* (Codd) Van Jaarsv. & T.J.Edwards and *P. lucidus* (Benth.) Van Jaarsv. & T.J.Edwards are given new status, and *P. pentheri* (Gürke) Van Jaarsv. & T.J.Edwards is transferred to this genus from *Coleus* and recognized as a species.

INTRODUCTION

Plectranthus includes 45 southern African species which are found in the subtropical forests and savannas of the summer rainfall region. The genus was revised by Codd (1975, 1985) who recognized 44 species in southern Africa. Subsequent collections and additional information have resulted in the recognition of another species and three new infraspecific taxa which are described here. Two varieties are raised to species level and one species, originally described under *Coleus*, is transferred to *Plectranthus*. The newly described taxa belong to the subgenus *Plectranthus*.

1. *Plectranthus malvinus* Van Jaarsv. & T.J.Edwards sp. nov. a *P. ciliatus* E.Mey. ex Benth. foliis firmis, coriaceis, succulentis, marginibus serratis pagina foliorum strigosa floribusque malvinis differt.

TYPE.—Eastern Cape, 3129 (Port St Johns): Mount Sullivan, (–DA), *E. van Jaarsveld & Bingham 10522* (NBG, holo.).

Decumbent, strigose, mat-forming herb; roots shallow, fibrous. *Stems* 4-angled, purple-green, ± 3 mm in diameter, strigose (white multicellular hairs), punctate; internodes 10–40 mm apart. *Leaves* fleshy, firm, ovate to obovate, 40–90 \times 30–50 mm, strigose, serrate with 8–10 pairs of teeth; abaxial surface strigose, veins purple, densely strigose, hairs white, gland dots colourless, sunken; base cuneate, apex acute; petiole 5–10 mm long, purple, densely villose on adaxial surface, decurrent. *Inflorescence* a raceme or lax panicle, 180–210 mm long; cymes 3-flowered, 10–15 mm apart; bracts ovate-lanceolate, 7 \times 2 mm long; pedicels ± 10 mm long. *Calyx* 4 mm long (enlarging to 10 mm), upper lobe ovate, 2 mm long (5 mm in fruit), lower lobes 4, linear, 1.5 mm long (4 mm after flowering). *Corolla* ± 12 mm long, pink (violet group 84c), tube laterally compressed, 6 mm long, saccate at base and 3 mm deep, narrowing to 2 mm at throat,

upper lip 7 mm long, 2-lobed, lateral lobes 3 mm long, lower lip boat-shaped, 5 mm long. *Nutlets* brown to black, ovoid, 1.5 \times 1.0 mm. *Flowering time:* March to May. Figure 1.

This species was collected along forest fringes on quartzitic sandstones of Mount Sullivan (W end). It has been cultivated as a ground cover at Kirstenbosch National Botanical Garden for a number of years under the name *P. ciliatus* 'Bingham'. Codd (1975) related this



FIGURE 1.—*P. malvinus*, *E. van Jaarsveld & Bingham 10522*, Port St Johns, Eastern Cape. Habit, $\times 0.5$. Scale bar: 12 mm. Artist: Vicky Thomas.

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MS. received: 1996-04-20.

taxon both to *P. strigosus* and *P. ciliatus*. It is distinguished by its firm, succulent, ovate to obovate leaves which are serrate, have densely pilose purple veins and are densely punctate underneath. The latter feature immediately separates it from *P. strigosus* or *P. lucidus* which have red gland dots. The flowers are reminiscent of *P. ciliatus* but are generally smaller and are an attractive mauve. *P. ciliatus* has soft leaves and usually bears white flowers.

P. malvinus is one of the endemics of the region of quartzitic sandstone in KwaZulu-Natal and northern Eastern Cape. It is found on Mount Thesiger, Mount Sullivan and in adjacent territory on forest margins. Associated species in the habitat include *Mitriostigma axillare*, *Drimiopsis maculata* and *P. ciliatus*.

2. *Plectranthus purpuratus* Harv., Thesaurus capensis 1: 53, t. 83 (1859). Type: ex Hort., Kew, from seed sent from Port Natal [KwaZulu-Natal: Durban], *R. Vause* s.n. (K, holo.!).

Procumbent to decumbent, perennial, succulent herb, up to 200 mm high; roots fibrous. *Stems* 4-angled, succulent. *Leaves* broadly trullate, broadly ovate, obovate to subrotund, 10–15 × 10–15 mm, entire to variably serrate to crenate with 2 or 3 pairs of teeth, strigose to subglabrous; lower surface occasionally purplish, rubropunctate; tip acute, base truncate to broadly cuneate; petioles 3–15 mm long. *Raceme* 30–290 mm long, racemose, occasionally with a pair of side branches; cymes 3-flowered, 5–10 mm apart; bracts linear-lanceolate, 3–4 mm long, persistent beyond flowering stage; pedicels 3–5 mm long. *Calyx* 3 mm long; fruiting calyx 5 mm long. *Corolla* 12–13 mm long, white or pale mauve, tube 5–8 mm long, basally ventricose, constricted about 3 mm from base and flared at throat, upper lobes emarginate, 3–5 mm long, lateral lobes ± 2 mm long, lower lip boat-shaped, 5–7 mm long. *Nutlets* brown or black, 1.5 mm long.

Plectranthus purpuratus is widely distributed in the eastern parts of southern Africa from Durban through KwaZulu-Natal and Swaziland to Mpumalanga (Eastern Transvaal), occurring in rocky gorges in savanna and grassland. The species has a diagnostic, medial constriction of the corolla tube which distinguishes it from *P. strigosus*, *P. lucidus* and *P. oertendahlii*.

Key to subspecies of *P. purpuratus*

- 1a Plants erect to decumbent; leaves entire to obscurely crenate, succulent, subrotund, subglabrous, subimbricate subsp. *purpuratus*
- 1b Plants procumbent; leaves not distinctly succulent, strigose, lax:
 - 2a Leaves large, trullate (petioles 12–15 mm long), distinctly serrate, with 3 or 4 pairs of teeth subsp. *tongaensis*
 - 2b Leaves broadly ovate to obovate (petiole 6–12 mm long), shallowly serrate with 2 or 3 pairs of teeth . . . subsp. *montanus*

2a. *Plectranthus purpuratus* Harv. subsp. *purpuratus*

Stems erect to decumbent, succulent. *Leaves* subimbricate, subrotund to broadly ovate, succulent, 15–45 × 15–38 mm, grey-green, entire, occasionally shallowly cre-

nate, with 3 pairs of teeth, subglabrous, rubropunctate beneath, apex rounded, base truncate to cuneate. *Raceme* 30–120 mm long, often with a pair of side branches; cymes 3-flowered, 5–10 mm apart; bracts ovate-lanceolate, 2 mm long, persistent; pedicel 2–3 mm long; fruiting calyx 5 mm long. *Corolla* 10–11 mm long, white, tube ± 4 mm long, constricted in middle. *Nutlets* brown, 1 mm long. Figure 2.

P. purpuratus subsp. *purpuratus* is confined to the Durban-Pietermaritzburg region of central KwaZulu-Natal (Figure 3) and occurs on rocky outcrops or south-facing cliffs in bushveld. It is commonly found in association with species such as *Aloe arborescens*, *Gasteria croucheri* and *Plectranthus hadiensis* var. *tomentosus*.

Subsp. *purpuratus* is distinguished from subsp. *montanus* and subsp. *tongaensis* by its decumbent habit and succulent, glabrescent, subrotund leaves which are crowded and often subimbricate. Its leaves are entire or, rarely, obscurely crenate. The typical subspecies was named for its purple abaxial leaf surfaces. The plants have an erect to decumbent habit.

2b. *Plectranthus purpuratus* subsp. *tongaensis* Van Jaarsv. & T.J. Edwards subsp. nov. a subspecies typica



FIGURE 2.—*P. purpuratus* subsp. *purpuratus*, E. van Jaarsveld 9843, Mamba Valley, KwaZulu-Natal. Plant, × 0.5. Scale bar: 10 mm. Artist: Vicky Thomas.

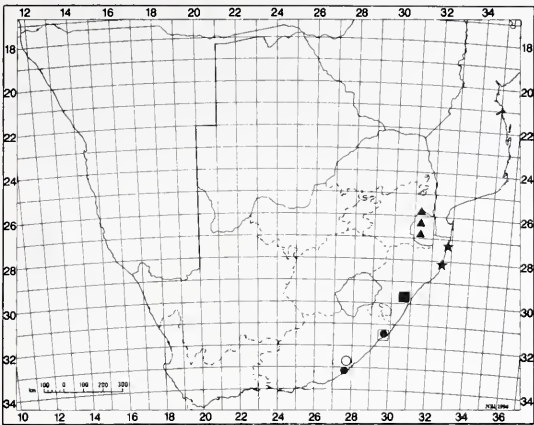


FIGURE 3.—Distribution of *P. lucidus*, ●; *P. purpuratus* subsp. *purpuratus*, ■; *P. purpuratus* subsp. *tongaensis*, ★; *P. purpuratus* subsp. *montanus*, ▲; *P. pentheri*, ○.

habitu procumbenti foliisque trullatis non congestis, marginibus serratis paribus dentium tribus vel quatuor differt.

TYPE.—KwaZulu-Natal, 2732 (Ubombo): Kosi Bay, (–BB), *Van Jaarsveld 12206* (NBG, holo.).

Procumbent, pubescent to glabrescent, succulent herb, rooting at nodes. *Stems* 4-angled, purplish to green, 2–3 mm in diameter, strigose (purplish to white hairs), rubropunctate; internodes 20–30(–60) mm long. *Leaves* ovate to broadly ovate, 30–34 × 15–18 mm, green or purple tinged, coarsely serrate, with 3 or 4 pairs of shallow teeth, abaxial surface strigose to glabrescent, rubropunctate, veins densely strigose, apex acute, base broadly cuneate; petiole 12–15 mm long, strigose, rubropunctate. *Raceme* 140–290 mm long, occasionally with a pair of basal side branches; cymes 3-flowered, 8–20 mm apart; bracts ovate-lanceolate, ± 3 mm long; pedicel ± 4 mm long. *Calyx* ± 3 mm long, enlarging to 6 mm, upper lip ovate, 2 mm long (± 4 mm after flowering), lower lobes 4, linear, ± 1.5 mm long (± 3.5 mm long after flowering), densely strigose (flushed with blue). *Corolla* 12–13 mm long, white, bilabiate, tube basally saccate, 7 mm long, upper lip 5–6 mm long, 2-lobed, lateral lobes 2–3 mm long, lower lip boat-shaped, 5–6 mm long. *Nutlets* black, ovoid, 1.5 × 1.0 mm. *Flowering time*: March to May. Figure 4A.



FIGURE 4.—*P. purpuratus*: A, subsp. *tongaensis*, *E. van Jaarsveld, Van der Walt & Crous 50*, Kosi Bay, KwaZulu-Natal; B, subsp. *montanus*, *E. van Jaarsveld 3386*, Barberton, Mpumalanga. A, B, habit, × 0.7. Scale bars: 14 mm. Artist: Vicky Thomas.



FIGURE 5.—*P. saccatus*: A–C, subsp. *saccatus*; D, subsp. *pondoensis*, *E. van Jaarsveld* 2201, Oribi Gorge, KwaZulu-Natal. Habit, $\times 0.5$. Artist: Vicky Thomas.

This subspecies is locally common or sporadic in coastal sand forest from St Lucia to Kosi Bay in northern KwaZulu-Natal (Figure 3). Plants are often found in association with *Crassula expansa* subsp. *fragilis*, *Plectranthus petiolaris* and *Cussonia arenicola*.

2c. *Plectranthus purpuratus* subsp. *montanus* *Van Jaarsv. & T.J. Edwards* subsp. nov. a subspecie typica foliis non congestis laminis obovatis marginibus vix serratis paribus dentium duobus differt.

TYPE.—Swaziland, 2631 (Mbabane): Mbabane, (–AC), *Compton* 32207 (NBG, holo.).

Procumbent, pubescent, succulent herb; roots shallow, fibrous. *Stems* 4-angled, purplish to green, 2.5 mm in diameter, strigose, rubropunctate; internodes 5–12 mm long. *Leaves* ovate to broadly ovate, 12–15 \times 10–15 mm, green to purplish, teeth (2 pairs) shallow, serrate to crenate-dentate, abaxial surface sparsely strigose, rubropunctate, veins densely strigose, base cuneate, apex obtuse to acute; petiole 6–12 mm long, strigose, rubropunctate. *Raceme* 30–100 mm long, occasionally with a pair of side branches at base; cymes 3-flowered, 5–12 mm apart; bracts ovate-lanceolate, \pm 2 mm long; pedicels 2–4 mm long. *Calyx* 3 mm long, enlarging to 6 mm; upper lobe 2 mm long (4 mm after flowering), ovate and lower lobes 4, linear, \pm 1.5 mm long (3.5 mm after flowering), densely strigose. *Corolla* 14–15 mm long, white, tube 7 mm long, upper lip 5–6 mm long, 2-lobed, lower lip boat-shaped, 3–4 mm long. *Nutlets* black, ovoid, 1.5 \times 1.0 mm. *Flowering time*: March to May. Figure 4B.

The obovate leaves of this subspecies are usually covered in a grey indumentum. The lamina margin is obscurely serrate with two pairs of teeth. The subspecies occurs along the Mpumalanga (Eastern Transvaal) Drakensberg (Figure 3), usually among rocks in grassland and forest margins. Associated species include *Aloe suprafoliata* and *P. verticillatus*.

3. *Plectranthus saccatus* Benth. subsp. *pondoensis* *Van Jaarsv. & S. Milstein* subsp. nov. a subspecie typica foliis manifeste succulentis, inflorescentia brevi, tuboque corollae brevi 6–7 mm longo differt.

TYPE.—KwaZulu-Natal, 3030 (Port Shepstone): Oribi Gorge, (–CA), *E. van Jaarsveld* 2201 (PRE, holo.).

Trailing, glutinous succulent herb. *Stems* obscurely four-angled; young stems 2–5 mm in diameter, purplish, minutely glandular pubescent, becoming glabrous; older stems striate; internodes 6–40 mm long. *Leaves* ovate to broadly trullate, 12–27 \times 10–28, both surfaces minutely glandular pubescent, abaxial surface slightly costate; petiole 5–25 mm long. *Racemes* secund, 30–50 mm long; bracts linear, \pm 1 mm long, caducous; pedicels 6–7 mm long. *Calyx* 3–6 mm long (enlarging to 8 mm), upper lip ascending, ovate, 1 mm long, lower lobes 4, narrowly linear-lanceolate, 1 mm long. *Corolla* saccate, tube 6–20 \times 3–7 mm, upper lip 2-lobed, 9–13 \times 7–12 mm, erect, lobes folded back, lower lip horizontal or slightly drooping, blue to pale mauve-pink, inner surface speckled with purple (often in 4 rows), lower lip 8 mm long, speckled with purple. *Stamens* \pm 14 mm long, declinate in lower lip, free for 8 mm; anthers purple, bent upwards. *Style* 11–12 mm long. Figure 5D.

P. saccatus subsp. *pondoensis* is distinguished from the typical subspecies by its distinctly succulent leaves and decumbent to procumbent habit with flexible stems up to 4 m long. The secondary growth of the species is anomalous with many broad collenchymatous rays which impart flexibility.

The two subspecies are ecologically separated, with subsp. *pondoensis* being common in scrub along gorge lips, and subsp. *saccatus* being common in forest. Succulence occurs in a number of cliff-dwelling species (*P. ernstii*, *P. purpuratus* and *P. strigosus*). The two subspecies maintain their vegetative characteristics under uniform cultivation. No hybrids between them have been observed.

P. saccatus subsp. *pondoensis* is restricted to the quartzitic sandstone cliff faces of the Msikaba River of northern Eastern Cape (northern Transkei) and southern KwaZulu-Natal (Figure 6). Associated species include *Cryptocarya wyliei* and *Crassula sarmentosa* var. *sarmentosa*.

P. saccatus subsp. *saccatus* is very variable, with several local forms (Figure 5A–C). The recognition of var. *longitubus* Codd within this species is contentious. The corolla tube length is highly variable and appears to form a continuum.

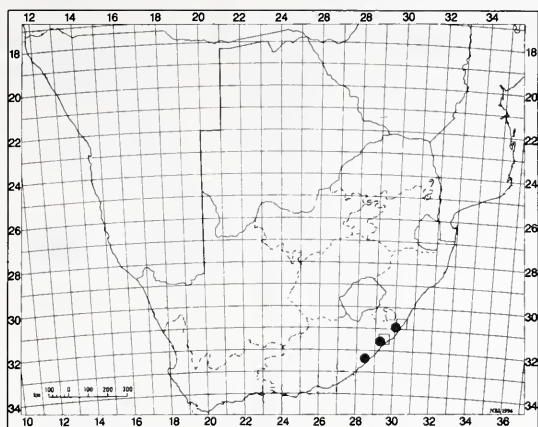


FIGURE 6.—Distribution of *P. aliciae*, ●; *P. saccatus* subsp. *pondoensis*, □.

4. ***Plectranthus aliciae*** (Codd) Van Jaarsv. & T.J.Edwards stat. nov. Type: Transkei, Butterworth, Kentani, Pegler 909 (PRE, holo.!).

P. madagascariensis var. *aliciae* Codd in Bothalia 11: 404 (1975).

Erect to decumbent, soft, semi-succulent herb to 400 mm high. *Leaves* 25–40 × 22–40 mm, broadly ovate, sparsely strigose, adaxial surface rubropunctate, serrate, teeth in 3 or 4 pairs, base truncate, apex acute. *Raceme* up to 130 mm long; cymes 3–6-flowered. *Calyx* 3 mm long (enlarging to 5 mm). *Corolla* white, 5–14 mm long, tube widening to throat. *Nutlets* 1 mm long, light to dark brown. Figure 7.

P. aliciae is distinguished by its ascending habit, membranous, sparsely pubescent lamina with 2 or 3 pairs of teeth and short corolla tube. It is distributed from East London to southern KwaZulu-Natal (Figure 6) occurring in subtropical lowland forest. Associated species at Oribi Gorge include *Cryptocarya woodii*, *P. oertendahlii*, *P. oribiensis*, *P. zuluensis* and *P. petiolaris*.

P. aliciae is sympatric with *P. madagascariensis* and is therefore accorded specific status. *P. madagascariensis* is a species of open subtropical thickets and forms dense stands, whereas *P. aliciae* is a forest dweller and retains its habit in cultivation. *P. aliciae* commemorates Alice Pegler (1861–1929), teacher and amateur botanist in the E Cape.

5. ***Plectranthus lucidus*** Van Jaarsv. & T.J.Edwards stat. nov. Type: Eastern Cape, Bathurst, Burchell 3924, (K!, holo.).

P. strigosus Benth. var. *lucidus* Benth. 12: 68 (1848).

Procumbent, succulent herb, rooting at nodes, glabrous or sparsely pubescent; roots fibrous. *Stems* 4-angled, purplish to green, 2.5 mm in diameter, strigose (white multicellular hairs), rubropunctate; internodes 5–20 mm long. *Leaves* ovate to broadly ovate, 12–15 × 10–15 mm, serrate to crenate-dentate, with 3 or 4 pairs of teeth, green to purplish, abaxial surface sparsely strigose, veins densely strigose, rubropunctate, base cuneate, apex obtuse to acute; petioles 5–15 mm long, strigose and rubropunctate.

Raceme simple, 30–100 mm long, rarely with a pair of side branches; cymes 1-flowered, verticillasters 5–10 mm apart; bracts ovate-lanceolate, 2–3 mm long; pedicel 4–5 mm long. *Calyx* at flowering 3–4 mm long, enlarging to 7 mm, consisting of a large, ovate upper lip 2 mm long (4 mm after flowering) and 4 subulate lower lobes, 3.5 mm long (5 mm long after flowering), densely strigose, with longer purplish hairs. *Corolla* 9–11 mm long, white or mauve; tube straight, 5 mm long, basally saccate, constricted distally; upper lip 5 mm long, 2-lobed, upper lobes 3 mm long, lateral lobes 2 mm long, with long multicellular white hairs, lower lip boat-shaped, margins strongly involute. *Nutlets* brown to black, ovoid, 1.5 × 1.0 mm. *Flowering time*: March to May. Figure 8.

Plectranthus lucidus forms mats on stabilized coastal sand dunes below trees (with mainly *Mimusops obovata* and *Allophylus natalensis*), from Bathurst in the south-eastern part to Port St Johns in the northeastern part of Eastern Cape. It shares its habitat with other shade-loving coastal plant species such as *P. madagascariensis* and *Scadoxus membranaceus*.

P. lucidus is closely related to *P. verticillatus* (L.f.) Druce and *P. strigosus* Benth. (section *Plectranthus* series *Plectranthus*); it is distinguished by its 2-flowered verticillasters and short corolla (9–11 mm) of which the lower lip margins are conspicuously involute. In both *P. strigosus* and *P. lucidus* the corolla is constricted at the throat, unlike *P. verticillatus* where the corolla is linear.

6. ***Plectranthus pentheri*** (Gürke) Van Jaarsv. & T.J.Edwards comb. nov. Type: Eastern Cape, Albany Dis-



FIGURE 7.—*P. aliciae*, Umtamvuna, KwaZulu-Natal. E. van Jaarsveld & Campher 117. Plant, × 0.5; habit much reduced. Scale bar: 20 mm. Artist: Vicky Thomas.



FIGURE 8.—*P. lucidus*, E. van Jaarsveld 3827, Port St Johns, Eastern Cape. Plant, $\times 0.6$; flowers and calyx, $\times 1.3$. Artist: Vicky Thomas.

trict, Breakfast Vlei, *Krook in Herb. Penther 1716* (W, holo.; PRE!).

Coleus pentheri Gürke in *Annalen des Naturhistorischen Museums in Wien* 20: 48 (1905).

Decumbent, succulent herb up to 100 mm tall; basal tuber 30×15 mm, white. *Stems* 4-angled, 2–4 mm in diameter, sparsely pilose, punctate, glands orange; internodes 3–6 mm long. *Leaves* conduplicate, succulent, firm, ovate to subrotund, 9–14 \times 9–14 mm, entire to dentate-serrate in upper half, teeth shallow, in 4 or 5 pairs; sparsely pubescent, punctate, glands orange, base broadly cuneate, apex obtuse; petiole 2 mm long. *Raceme* 50–70 mm long, simple; cymes 3-flowered, 5–10 mm apart; bracts broadly ovate to subrotund, mucronate, 4 \times 4 mm, initially imbricate, caducous; pedicels 5 mm long. *Calyx* 3 mm long (enlarging to 5 mm), upper lip broadly ovate, 2.0 \times 2.5 mm, lower lobes 4, linear, 2 mm long. *Corolla* 15 mm long, white; tube laterally compressed, slightly geniculate, 5.0 \times 1.5 mm, expanding to 3 mm at throat, upper lip 3 mm long, 2-lobed, lateral lobes 2.5 mm long, lower lip



FIGURE 9.—*P. pentheri*, E. van Jaarsveld, Sardien & Peterson 13774, Kei River, Eastern Cape. Plant and rootstock, $\times 0.5$. Scale bar: 20 mm. Artist: Vicky Thomas.

boat-shaped, 9 mm long. *Nutlets* brown to black, ovoid, 1.5 \times 1.0 mm. *Flowering time*: March to May. Figure 9.

Codd (1985) regarded *P. pentheri* (as *Coleus pentheri*) as a synonym of *P. neochilus*. The two entities, however, differ markedly. Both belong to subgenus *Calceolanthus* but *P. pentheri* is at once distinguished by its oblong tuberous roots and white flowers. It also lacks the strong aroma of the closely related *P. neochilus*, which is a widespread species with fibrous roots and mauve to purple flowers.

P. pentheri is known from a few gatherings. It grows with *Crassula ericoides* on lithosols of granite boulders in grassland.

ACKNOWLEDGEMENTS

Dr O. A. Leistner is thanked for preparing the Latin diagnoses and editing the text.

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Five new species of *Lachenalia* (Hyacinthaceae) from arid areas of South Africa

G.D. DUNCAN*

Keywords: Hyacinthaceae, *Lachenalia*, new species, South Africa

ABSTRACT

Five new species of *Lachenalia* are described: *L. aurioliae* G.D.Duncan from the Little Karoo and Great Karoo, *L. obscura* Schltr. ex G.D.Duncan from Namaqualand, the Kamiesberg, the western Great Karoo and the Little Karoo, *L. inconspicua* G.D.Duncan from the Kamiesberg, western Bushmanland and southern Namaqualand, *L. marlothii* W.F.Barker ex G.D.Duncan from the Calvinia-Sutherland region of the western Great Karoo, and *L. xerophila* Schltr. ex G.D.Duncan from northwestern and central Namaqualand, and western Bushmanland.

INTRODUCTION

This is the second in a series of papers on new species of *Lachenalia*, and serves as a continuation of the recent work of W.F.Barker (Barker 1978, 1979, 1983a & b, 1984, 1987, 1989) and the current author (Duncan 1987, 1988a & b, 1989, 1992, 1993, 1994, 1996), towards a revision of the genus. Material of a number of unpublished *Lachenalia* species has languished in local and foreign herbaria for many years, and in some instances manuscript names accompany this material; the abovementioned papers serve as a means of validating these names, where it is considered expedient. Furthermore, new species are published which have come to light in recent years. In most instances, the new species are described from both dried and living material, the dried material extracted mainly from the extensive *Lachenalia* holdings at the Compton Herbarium at Kirstenbosch (NBG), and the living material both from the wild and the large collection maintained in the nursery at Kirstenbosch National Botanical Garden.

Lachenalia aurioliae G.D.Duncan, sp. nov. *L. schelpei* W.F. Barker affinis ob flores similes subspicatos oblongo-urceolatos, stamina parum exserta foliaque lanceolata; sed segmentis interioribus perianthii multo longioribus, staminibus declinatis folioque conduplicato immaculato plerumque costa distincta differt.

TYPE.—Western Cape, 3222 (Beaufort West): hillside facing Hesperus Old Age Home, Beaufort West, (–BC), 26-6-1984, A. Batten 468 (NBG, holo.!: PRE).

Deciduous, winter-growing geophyte 45–120 mm high. *Bulb* subglobose, 20–25 mm in diam., surrounded by thin, pale to dark brown spongy outer tunics, produced into a short neck. *Leaves* 1 or 2, partially to fully conduplicate, lanceolate to ovate-lanceolate with a distinct midrib and faint depressed longitudinal veins on upper surface, yellowish green, plain or faintly spotted with dull

green or purple on upper surface, with darker green blotches and transverse bands on lower surface, merging into brownish magenta transverse bands on the loosely clasping leaf bases. *Inflorescence* subspicate, moderately dense, few to many-flowered, 35–90 mm long, with a short sterile tip; peduncle suberect to erect, fairly sturdy, 45–140 mm long, pale green with distinct, irregularly scattered brownish magenta blotches in lower half, and minute spots in upper half; rachis pale green in lower half, shading to pale greenish brown in upper half, mottled with tiny brownish magenta specks; pedicels absent or up to 1 mm long; bracts ovate to lanceolate, greenish white, with or without pale brownish magenta tips, 1–4 × 1–3 mm. *Flowers* patent to cernuous, oblong-urceolate, pale bluish white to yellowish white, fading to dull reddish brown; outer perianth segments swollen at base, oblong, 6–7 × 4–5 mm, minutely spotted with dark blue on keel and near apex, pale bluish white to yellowish white with distinct dull reddish brown to purplish brown gibbosities; inner perianth segments obovate, 9–10 × 5 mm, translucent white with a dark blue or brownish blue keel, with or without a dull reddish purple zone near apex. *Stamens* very slightly exserted, declinate; filaments white, 8–9 mm long. *Ovary* ovoid, pale green, 3 × 2 mm; style white, 7–8 mm long, protruding beyond stamens as ovary enlarges. *Capsule* ovoid, membranous, 6–8 × 5 mm. *Seed* ovoid, shiny black, 2 mm long, with a ridged terminal arillode 1 mm long. Figures 1A; 2 & 3.

Etymology: named after Mrs Auriol Batten, whose collection forms the type material of this species, in recognition of her contribution to the knowledge of South Africa's flora through her superb watercolour paintings which have illustrated several books authored or co-authored by her.

Diagnostic characters

L. aurioliae is characterised by a subspicate inflorescence of cernuous or patent, oblong-urceolate flowers with the translucent white inner perianth segments distinctly longer than the outer ones. The declinate stamens are very slightly exserted beyond the tip of the perianth and the plant usually has two lanceolate or ovate-lanceolate leaves which are partially to fully conduplicate, usually with a distinct midrib.

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MS. received: 1996-11-08.

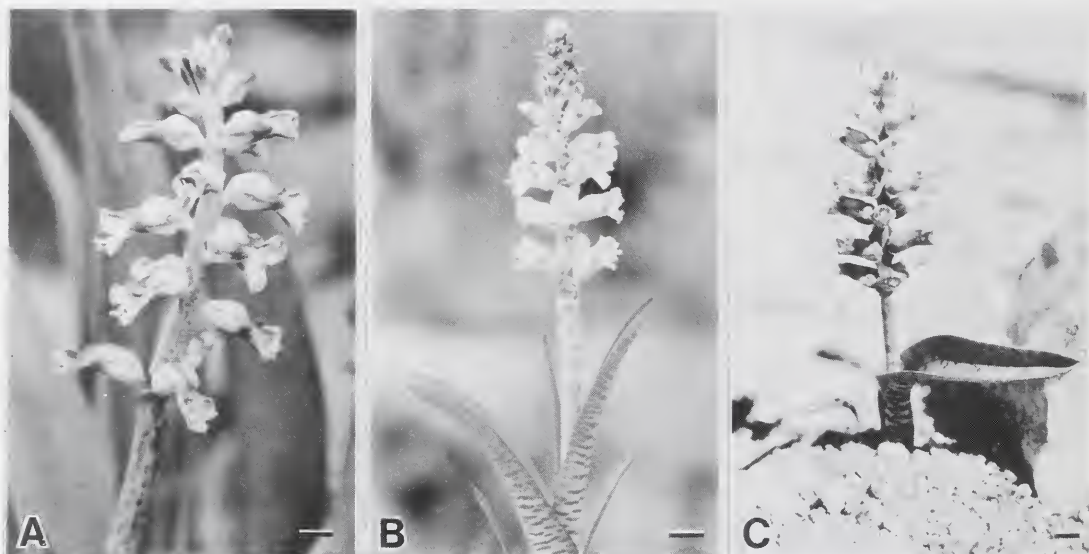


FIGURE 1.—A, *Lachenalia aurioliae*, Batten 468; B, *L. obscura*, Duncan 108; C, *L. inconspicua*, Duncan 259. Scale bars: 10 mm.

The upper leaf surface may be plain or spotted with dull green or purple, and the lower surface with or without darker green blotches and transverse bands.

L. aurioliae is related to *L. schelpei* W.F.Barker, (at present known only from the Hantam Mountains at Calvinia in the Northern Cape), in that both species have patent or cernuous oblong-urceolate flowers borne on very short pedicels, with very slightly exerted stamens and similar lanceolate leaves. In *L. schelpei*, the flowers are subtended by conspicuous, long, narrowly lanceolate bracts, and the inner perianth segments are only slightly longer than the outer segments, as compared to the very short, ovate to lanceolate bracts and distinctly longer inner perianth segments of *L. aurioliae*. Furthermore, the stamens of *L. schelpei* are arranged symmetrically around the rim of the mouth of the perianth, whereas in *L. aurioliae* the stamens are distinctly declinate. The flower colour of *L. aurioliae* varies from pale bluish white to yellowish white whereas *L. schelpei* has greenish white flowers. The two species are geographically clearly separated. *Flowering time*: June to August.

Distribution and habitat

Material of *L. aurioliae* was collected for the first time by C. Thorne in October 1935 at Leeuwkloof in the Nuweveld Mountains north of Beaufort West. It is a variable, early flowering species with a fairly wide distribution in the southern Great Karoo and the Little Karoo, where it is found in a variety of arid habitats ranging from sandy river courses in full sun to south-facing hill slopes in heavy soil. At a locality near Whitehill Station in the Little Karoo it grows together with the very distinctive *L. whitehillensis* W.F.Barker, another Karoo endemic species which flowers much later in the year.

Material examined

NORTHERN CAPE.—3221 (Merweville): between Boschluisloof and Prince Albert, (–AB), July 1954, *Stokoe s.n.* (SAM); west of Steenbokkraal, (–BA), June 1986, *Bayer 5189* (NBG).

WESTERN CAPE.—3222 (Beaufort West): Leeuwkloof, Nieuweveld, (–BA), Oct. 1935, *Thorne s.n.* (SAM); 16 km S of Beaufort West, (–BC), July 1986, *Van Zijl s.n.* (NBG); hillside facing Hesperus Old Age Home, Beaufort West, (–BC), June 1984, *Batten 468* (NBG). 3320 (Montagu): in river course at Whitehill Station, (–BA), Aug. 1986, *Duncan 243* (NBG); Ratelfontein, between Montagu and Kareevlakte, (–CB), July

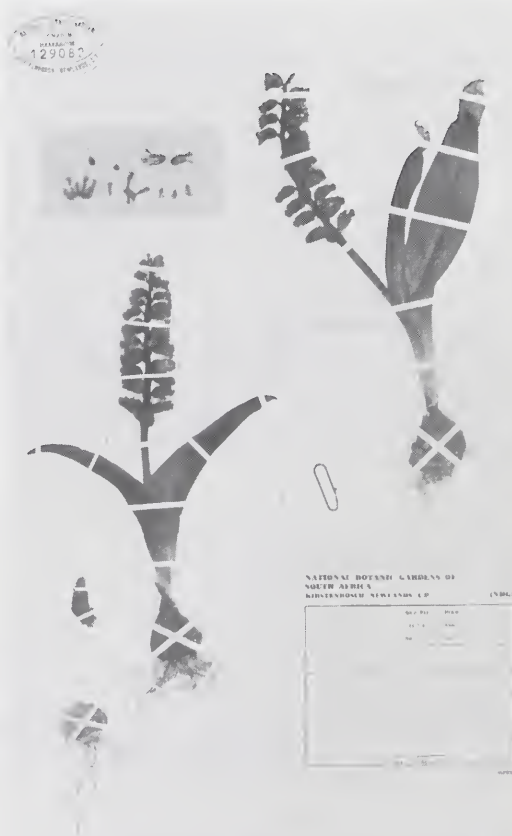


FIGURE 2.—Holotype of *Lachenalia aurioliae*, Batten 468.

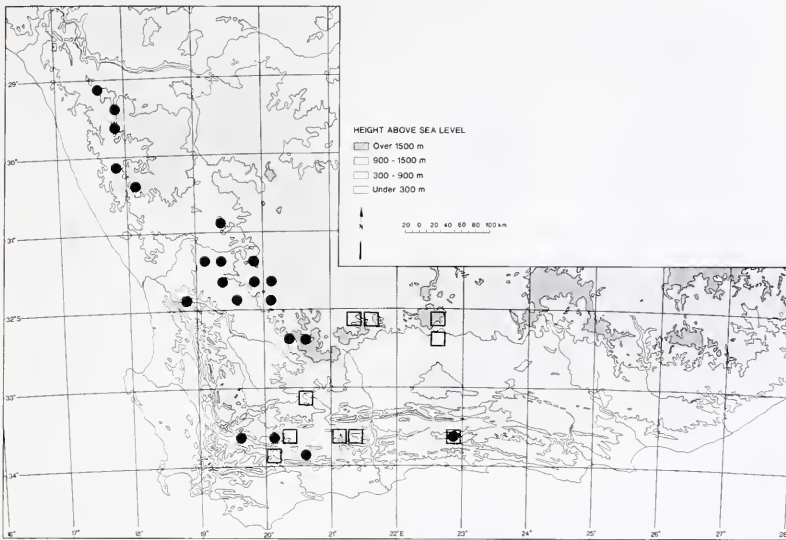


FIGURE 3.—Distribution of *Lachenalia auriolae*, □; *L. obscura*, ●

1954, *Lewis 4397* (SAM); Wildehondekloof Pass, 36 km E of Montagu, (–CC), Aug. 1974, *Nordenstam & Lundgren 1191* (NBG). 3321 (Ladismith): Mannshoop Farm, 0.8 km from homestead, (–CA), July 1982, *Laidler 186* (NBG); N of Rooiberg, Ladismith, (–CB), Aug. 1954, *Wurts 1227* (NBG). 3322 (Oudtshoorn): hills near Kammanassie, (–DB), July 1954, *Lewis 4396* (SAM).

***Lachenalia obscura* Schltr. ex G.D.Duncan, sp. nov.** *L. maximiliani* Schltr. ex W.F. Barker affinis ob segmentos interiores perianthii similes ad apicem magenteos, folium lanceolatum, bulbum globosum squamis exterioribus duris brunneis circumcinctum, seminaeque globosa; sed planta omnino grandiora floribus oblongo-campanulatis pallide flavo-virentibus ad brunneolocaeruleis vel cremeis, staminibus parum exsertis folisque plerumque pagina inferiora fasciis distinctis viridibus, brunneolo-purpureis et magenteis differt.

TYPE.—Northern Cape, 3119 (Calvinia): Vogelstruis Vlakte, Calvinia Division, (–DC), 26-7-1941, *R.H. Compton 11174* (NBG, holo.!).

Deciduous, winter-growing geophyte 55–380 mm high. *Bulb* globose, 10–25 mm in diam., white, surrounded by hard, cartilaginous pale to dark brown outer scales, produced into a short, strawlike neck. *Leaves* usually 2, erect to suberect, yellowish green to dark green, often conduplicate, 25–280 × 5–45 mm, upper leaf surface with faint, depressed longitudinal veins, usually unmarked, lower leaf surface usually heavily banded with bright green merging into dull brownish purple and magenta on clasping leaf base. *Inflorescence* spicate to subspicate, 15–220 mm long, few to many-flowered, with a short sterile tip; flowers often arranged in distinct whorls of three at base of inflorescence, becoming less distinctly whorled towards top of inflorescence; peduncle erect to suberect, slender or sturdy, 25–100 mm long, pale to dark green with pale to dark purplish blotches; rachis mottled with very pale bluish purple; pedicels white, often absent in lower half of inflorescence, but up to 2 mm long in upper part; bracts ovate to lanceolate, greenish white, 2–4 × 1–3 mm. *Flowers* patent to slightly cernuous, oblong-campanulate, pale yellowish green to brownish blue

or cream, with or without distinct magenta tips, fading to dull purple; outer perianth segments oblong, 6–9 × 4 mm, pale yellowish green to brownish blue or cream with pale blue speckles or solid blue at base, with dull brown, brownish purple or green gibbosities and slightly recurved tips; inner perianth segments protruding well beyond outer segments, obovate, translucent white with distinct bright



FIGURE 4.—Holotype of *Lachenalia obscura*, Compton 11174.



FIGURE 5.—Painting of *Lachenalia obscura*, drawn from Compton 11174, reproduced from the original watercolour by Miss W.F. Barker. Plant, $\times 0.7$.

green keels, recurved, with or without pale to dark magenta tips, $8-10 \times 5-7$ mm. *Stamens* declinate, as long as or shortly exserted up to 2 mm beyond inner perianth segments; filaments white, $8-11$ mm long. *Ovary* ovoid, pale green, $3-4 \times 2$ mm; style white, 8 mm long, protruding beyond stamens as ovary enlarges. *Capsule* ovoid, $7-8 \times 4-6$ mm. *Seed* globose, 1 mm long, shiny black, with a short, ridged terminal arillode 0.3 mm long. Figures 1B; 3-5.

Etymology: named *obscura* by Schlechter to convey the obscure and very variable appearance of this species.

Diagnostic characters

L. obscura is characterized by a spicate or subspicate inflorescence of patent to slightly cernuous, oblong-campanulate, pale yellowish green to brownish blue or cream flowers, with or without distinct magenta tips. The translucent white, inner perianth segments are distinctly longer

than the outer segments and have slightly recurved tips. The flowers are usually arranged in distinct, three-flowered whorls in the lower part of the inflorescence, becoming less distinctly whorled towards the top. The declinate stamens are included within, or very slightly exserted beyond the perianth. The one or two erect to suberect, lanceolate leaves usually have distinct green to brownish purple and magenta bands on the lower surface, and the globose bulb is surrounded by hard, dark brown, cartilaginous outer scales.

L. obscura appears to be most closely related to *L. maximiliani* Schltr. ex W.F.Barker, a dwarf species occurring in large colonies and restricted to the Wuppertal-Cederberg area of the Western Cape. Both species have spicate or subspicate inflorescences with magenta-tipped inner perianth segments and a globose bulb surrounded by hard, dark brown outer scales and similar globose seeds with a terminal, ridged arillode. *L. maximiliani* differs from *L. obscura* mainly in having narrow-urccolate, very pale blu-

ish grey flowers and a single unbanded, canaliculate leaf. *Flowering time*: June to October.

Distribution and habitat

Rudolf Schlechter collected this species for the first time at Papkuilsfontein, southeast of Vanrhynsdorp, in August 1897. He distributed material to nine local and foreign herbaria under his manuscript name *L. obscura*, where it has remained unpublished for one hundred years. *L. obscura* is a widely distributed and very variable species; it is currently recorded from Steinkopf at the northernmost end of its range, southwards throughout Namaqualand to the Kamiesberg and Knersvlakte, eastwards to the Nieuwoudtville-Calvinia area where it is common, and further south to Sutherland, and south and southeastwards to the Montagu and Oudtshoorn areas.

Due to its wide distribution, *L. obscura* is encountered in a wide variety of habitats, but is usually found on karroid flats in dry stony clay soil, and less frequently in sandy soil on moist lower mountain slopes. Plants usually grow singly or in small clumps in full sun among low-growing bushes. The typical forms of this species, such as those occurring in the Nieuwoudtville-Calvinia area, have pale yellowish green, oblong-campanulate flowers with distinct magenta tips and leaves with bright green to brownish purple and magenta bands on the lower leaf surface, whereas certain forms found further north in Namaqualand have longer, less campanulate flowers which are pale blue, with or without very pale magenta tips, and leaves without distinct bands on the lower surface.

Material examined

NORTHERN CAPE.—2917 (Springbok): Steinkopf Reserve, (–BA), Aug. 1980, *Van Berkel* 164 (NBG); Farm Ratelpoort, (–BD), Aug. 1971, *Hall* 4087 (NBG); Farm Eksteenfontein, (–DB), Aug. 1986, *Duncan* 252 (NBG). 3017 (Hondeklipbaai): Kamieskroon, (–BB), Aug. 1980, *Van Berkel* 166 (NBG). 3018 (Kamiesberg): Kamiesberg, (–AC), Aug. 1984, *Van Zijl s.n.*, (NBG); Studer's Pass, E of Garies, (–AC), June 1970, *Stayner s.n.* (NBG). 3019 (Loeriesfontein): N of Loeriesfontein, (–CD), July 1972, *Hiemstra s.n. sub NBG* 97199 (NBG). 3118 (Vanrhynsdorp): Farm Papkuilsfontein, 41 km SE of Vanrhynsdorp, (–DD), Aug. 1897, *Schlechter* 10907 (B, BM, G, GRA, K, L, PRE, S, Z). 3119 (Calvinia): Grasberg, N of Nieuwoudtville, (–AC), Aug. 1961, *Barker* 9351 (NBG); between Grasberg & Nieuwoudtville, (–AC), Aug. 1961, *Barker* 9362 (NBG); Klipkoppies, Nieuwoudtville, (–AC), Aug. 1961, *Barker* 9379 (NBG); Sept. 1971, *Hardich s.n.* (NBG); Nieuwoudtville Reserve, (–AC), July 1983, *Perry & Snijman* 2173 (NBG); E of Nieuwoudtville, (–AC), July 1970, *Nordenstam* 770 (NBG); Farm Uitkomst, NW of Nieuwoudtville, (–AC), Sept. 1970, *Barker* 10750 (NBG); Farm Soetwater, between Nieuwoudtville & Calvinia, (–AD), Aug. 1974, *Botha s.n.* (NBG); Akkerendam Nature Reserve, Calvinia, (–BD), July 1961, *Barker* 9321 (NBG); Calvinia commonage, (–BD), Aug. 1968, *Stayner s.n. sub NBG* 93582 (NBG); 30 km before Calvinia, on road from Karooport, (–BD), Sept. 1983, *Duncan* 108 (NBG); E of Calvinia, on road to Williston, (–BD), July 1973, *Thomas s.n. sub NBG* 98484 (NBG); Farm Vanrhynshoek, Calvinia, (–BD), *Thompson* 2366 (NBG); Lokenburg, (–CB), Aug. 1959, *Acocks* 20602 (NBG); W of Tafelberg, SE of Calvinia, (–DB), May 1975, *Thompson* 2445 (NBG); Vogelstruis Vlake, (–DC), July 1941, *Compton* 11174 (NBG); 3120 (Williston): 34 km on road from Middelpoos to Calvinia, (–CA), Oct. 1974, *Thomas s.n. sub NBG* 105715 (NBG); Farm Blomfontein, E of Middelpoos, (–CC), Aug. 1972, *Barker* 10784 (NBG); 3220 (Sutherland): Farm Voelfontein, Sutherland, (–AD), Sept. 1968, *Hall* 3252 (NBG); S of Sutherland, (–BC), Oct. 1968, *Hall* 3287 (NBG); near Sutherland, (–BC), Sept. 1969, *Stayner s.n. sub NBG* 93909 (NBG).

WESTERN CAPE.—3319 (Worcester): E of Worcester on Robertson road, (–DA), July 1954, *Barker* 8255 (NBG). 3320 (Montagu): Farm

Mooi-Erferis, NW of Montagu, (–CA), Oct. 1979, *Kriel s.n. sub NBG* 120475 (NBG); Flats E of Warmwaterberg, (–DC), Aug. 1971, *Boucher* 1576 (NBG). 3322 (Oudtshoorn): S slopes of Mannetjesberg, (–DB), Oct. 1971, *Oliver* 3605 (NBG).

***Lachenalia inconspicua* G.D.Duncan, sp. nov.** *L. concordianae* Schltr. ex W.F. Barker affinis ob habitum nanum similem, inflorescentiam spicatum floribus plerumque verticillis 3-floris, foliumque singularem lanceolatum pagina inferiora fasciis brunneo-viridibus; sed floribus oblongo-campanulatis, lacteis vel viridi-albis, folioque coriaceo late patenti pagina superiora maculis purpureo-brunneis differt.

TYPE.—Northern Cape, 2918 (Gamoep): 500 m beyond Gamoep, on road Springbok to Gamoep, in deep red gravelly sand at side of road, (–CD), 19-8-1986, *G.D. Duncan* 259 (NBG, holo.).

Deciduous, winter-growing geophyte 120–160 mm high. *Bulb* globose, 15–20 mm in diam., white with thick, spongy, dark brown outer tunics produced into a short neck. *Leaf* usually solitary, lanceolate or occasionally ovate, widely spreading, deeply channelled, leathery, 85–150 × 15–20 mm, glaucous with depressed longitudinal veins and irregularly scattered purplish brown spots on upper surface, and broad, brownish green bands on lower surface, shading to narrower brownish magenta bands on clasping leaf base. *Inflorescence* spicate or subspicate, fairly dense, few to many-flowered, 45–80 mm long, with a very short sterile tip, flowers usually arranged in distinct three-flowered verticils; peduncle erect, sturdy, pale green with large purplish brown blotches, 55–80 mm long; pedicels absent, bracts very much reduced, ovate, 1 mm long. *Flowers* erecto-patent, oblong-campanulate, pale bluish or greenish white, fading to dull brownish purple; outer perianth segments oblong, slightly recurved, pale greenish blue with darker blue markings at base, and dull purplish brown or brownish green gibbositities, 7–8 × 4–5 mm; inner perianth segments obovate, translucent white, with brownish green keels, protruding well beyond outer segments, slightly recurved, upper two segments overlapping, lower segment slightly longer, 8–11 × 4–5 mm. *Stamens* declinate; filaments white, 7–9 mm long, included within, or slightly exerted up to 1 mm beyond perianth. *Ovary* ovoid, pale green, 3 mm long; style white, 8–9 mm long. *Capsule* ovoid, membranous, 9–10 × 5 mm. *Seed* globose, 1 mm long, dull black, with a ridged terminal arilode 1 mm long. Figures 1C; 6 & 7.

Etymology: named for the inconspicuous, well-camouflaged flowers.

Diagnostic characters

L. inconspicua is a dwarf species characterized by a spicate or subspicate inflorescence of pale bluish white or greenish white oblong-campanulate flowers with purplish brown or brownish green gibbositities, usually arranged in distinct three-flowered verticils, and a usually solitary, lanceolate, widely spreading, deeply channelled leaf with conspicuous transverse bands on the tightly clasping leaf base. It is related to *L. concordiana* Schltr. ex W.F. Barker, another dwarf species with greenish cream flowers also arranged in three-flowered verticils; but the latter differs

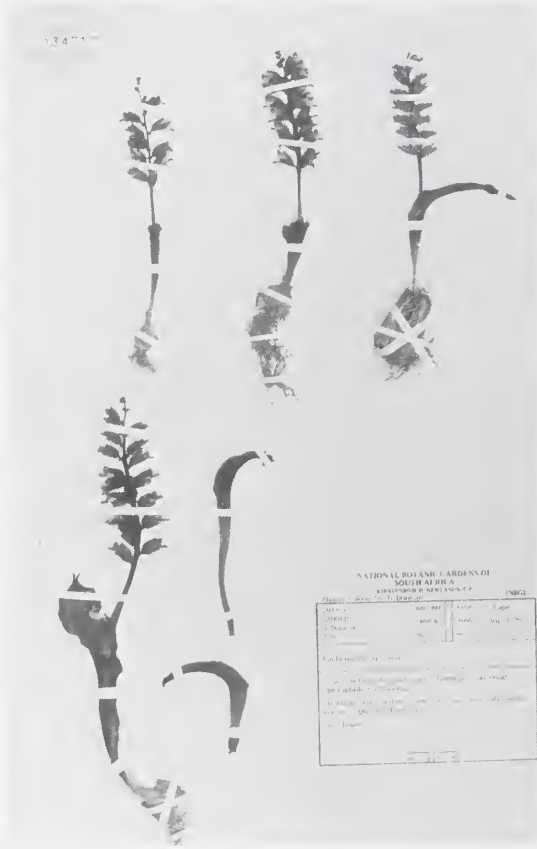


FIGURE 6.—Holotype of *Lachenalia inconspicua*, Duncan 259.

in having a linear-lanceolate leaf and widely campanulate flowers with dark green gibbosities and the tips of the inner and outer perianth segments all distinctly recurved. *Flowering time*: July to August.

Distribution and habitat

L. inconspicua is at present known only from a few collections made in the Kamiesberg, western Bushmanland and southern Namaqualand in the Northern Cape. According to current records, the first collection was made by F. Archer as recently as August 1982 NE of Gamoep, and it has since been found at several locations near Gamoep, and further south near Leliefontein, Kliprand and Bitterfontein. It is locally plentiful and occurs on open flats in deep red gravelly sand. An interesting growth feature of this species in cultivation is the manner in which healthy bulbs periodically remain completely dormant during the growing season, a characteristic shared by several *Lachenalia* species from the very arid parts of South Africa.

Material examined

NORTHERN CAPE.—2918 (Gamoep): 0.5 km beyond Gamoep, on road from Springbok to Gamoep, (–CD), Aug. 1986, *Duncan 259* (NBG); Kouberg, NE of Gamoep, (–CD), Aug. 1982, *Archer 192* (NBG); Vaalkoei Farm, SE of Gamoep, (–CD), Aug. 1996, *Duncan 381* (NBG); 3018 (Kamiesberg): 2 km S of Paulshoek village, (–AD), Sept. 1996, *Petersen*

41 (NBG); 5 km on R358 to Kliprand, (–CD), Aug. 1996, *Duncan 378* (NBG); 6 km SW of Kliprand, (–DA), Aug. 1995, *Symmonds 2* (NBG).

***Lachenalia marlothii* W.F.Barker ex G.D.Duncan**, sp. nov. *L. marginatae* W.F. Barker affinis ob folium singulare simile ovatum ad ovato-lanceolatum, coriaceum, basi amplexentis fasciis distinctis purpureo-brunneis, flores urceolato-oblongos, segmentosque interiores perianthii longos protrudentes; sed folio sine margine distincto coriaceo, basi arcte circumcincto, segmentis perianthii distincte recurvatis floribusque valde odoratis differt.

TYPE.—Northern Cape, 3119 (Calvinia): between Vlakkraal and Kalkgat Suid, S of Calvinia, (–DC), 23-7-1961, *W.F.Barker 9330* (NBG, holo.!).

Deciduous, winter-growing geophyte 90–160 mm high. *Bulb* subglobose, 15–33 mm in diam., white with brown spongy outer tunics. *Leaf* solitary, 30–60 × 10–25 mm, suberect, ovate to ovate-lanceolate, with an undulate, sometimes crisped margin, blade very leathery, dark green and unmarked on upper surface, with dark purplish brown and green transverse bands on lower surface; tightly clasping leaf base 30–70 mm long, white with very conspicuous purplish brown bands in the upper half, shading to magenta in the lower half. *Inflorescence* spicate or subspicate, fairly dense, few- to many-flowered, 40–95 mm

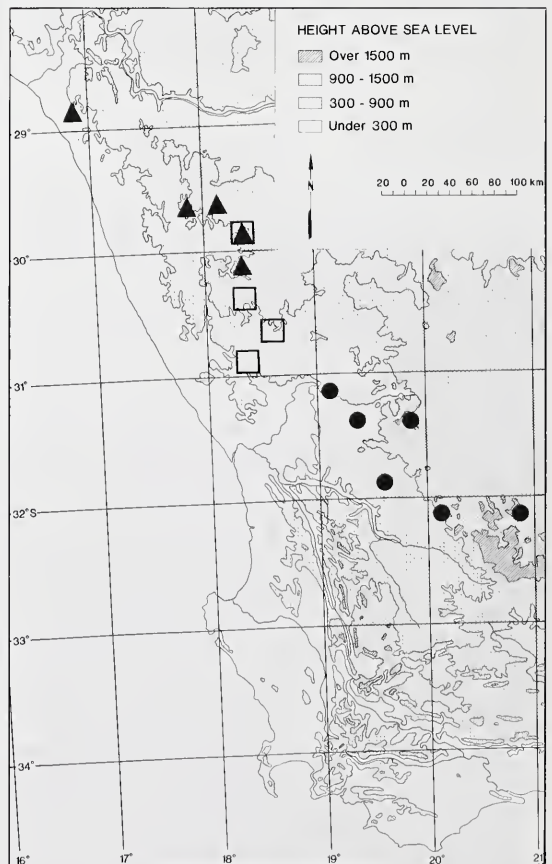


FIGURE 7.—Distribution of *Lachenalia inconspicua*, □; *L. marlothii*, ●; and *L. xerophila*, ▲.

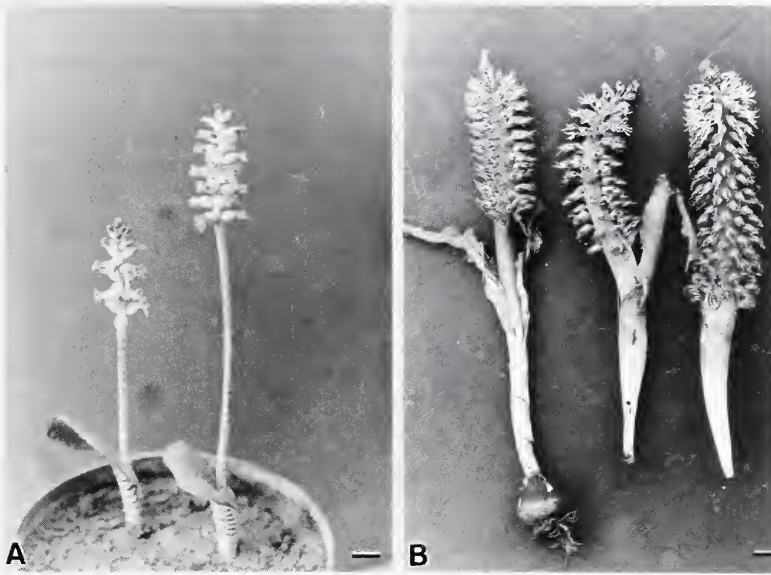


FIGURE 8.—A, *Lachenalia marlothii*, Botha s.n.; B, *L. xerophila*, Botha s.n. Scale bars: 10 mm.

long, with a very short sterile tip; peduncle slender, erect, 40–100 mm long, pale green with brownish purple blotches; pedicels absent or up to 2 mm long; bracts white, ovate, 1–2 mm long. *Flowers* strongly scented, patent or suberect, urceolate-oblong; outer perianth segments ovate, pale blue and green with darker blue bases, 8–9 × 5 mm, with greenish purple or purplish brown gibbosities and recurved tips; inner perianth segments obovate, 8–11 × 3–6 mm, white or brownish yellow with purplish green keels, protruding well beyond outer segments, recurved, upper two segments overlapping, lower segment longer and narrower. *Stamens* declinate; filaments white, 8–10 mm long, included within perianth. *Ovary* ovoid, pale green, 4–5 × 3–4 mm; style white, 6–7 mm long. *Capsule* ovoid, 5–6 × 4 mm. *Seed* ovoid, 1.5 mm long, shiny black with a ridged terminal arillode 0.5 mm long. Figures 7, 8A & 9.

Etymology: *L. marlothii* is named after the famous German chemist and botanist Rudolf Marloth, who made the first recorded collection of this species in October 1920.

Diagnostic characters

L. marlothii is characterized by a spicate or subspicate inflorescence of patent or suberect, pale blue and yellowish green urceolate-oblong flowers with recurved tips and included stamens, and a very distinctive, single, ovate to ovate-lanceolate, coriaceous, suberect leaf with a heavily banded, tightly clasping leaf base. The peduncle is heavily marked with brownish purple blotches and the flowers have a strong sweet scent.

L. marlothii appears to be most closely related to *L. marginata* W.F. Barker which also has an ovate or ovate-lanceolate, leathery leaf with distinct purplish brown bands on the clasping base, urceolate-oblong flowers with brownish gibbosities on the outer perianth segments and long protruding inner perianth segments. *L. marginata* differs in having a distinctly coriaceous leaf margin, the

clasping leaf base is not tight, the inner and outer perianth segments are not recurved, and the flowers are not heavily scented. *Flowering time:* July to September.



FIGURE 9.—Holotype of *Lachenalia marlothii*, Barker 9330.



FIGURE 10.—Holotype of *Lachenalia xerophila*, Botha s.n.

Distribution and habitat

L. marlothii was collected for the first time by Rudolf Marloth in October 1920 at Waterkloof in the Sutherland Roggeveld, which forms the southern boundary of its distribution. It has since been collected mainly in the Calvinia District, and is currently known from as far north as Brandkop, north of Nieuwoudtville. Plants occur singly or in groups and are usually associated with south-facing hillslopes in clay soil.

Material examined

NORTHERN CAPE—3119 (Calvinia): Brandkop, N of Nieuwoudtville, (–AA), Aug. 1950, *Barker 6486* (NBG); Calvinia road towards Soetwater turn-off, (–AD), July 1971, *Botha s.n.* (NBG); Van Rhynshoek Farm, Calvinia, (–BD), Oct. 1986, *Thomas 275*, (NBG); between Vlakkraal and Kalkgat Suid, S of Calvinia, (–DC), July 1961, *Barker 9330* (NBG). 3220 (Sutherland): Gannaga Pass, SW of Middelpas on Calvinia-Ceres road, (–AA), Sept. 1971, *Hardich s.n. sub. NBG 93862* (NBG); Waterkloof, Sutherland Roggeveld, (–BB), Oct. 1920, *Marloth 9661* (PRE).

***Lachenalia xerophila* Schltr. ex G.D.Duncan, sp. nov.** *L. klinghardtianae* Dinter et *L. physocaulotis* W.F. Barker affinis ob stamina similes bene exserta declinata, pedunculum rachidemque conspicue tumidum, inflores-

centiamque subspicatum vel racemosam floribus oblongo-campanulatis; sed inflorescentia multo densiora floribus minoribus cernuis gibbis distinctissimis magnis brunneis, folioque lanceolato-acuto canaliculato differt.

TYPE.—Northern Cape, 2918 (Gamoep): Kouberg Farm, off R355 Springbok to Gamoep, western Bushmanland, (–CD), 29-8-1972, *M.C.Botha s.n. sub. NBG 95451* (NBG, holo.!).

Deciduous, winter-growing geophyte 100–250 mm high. *Bulb* usually deep-seated, globose, 15–25 mm in diam., white with membranous dark brown outer tunics. *Leaves* one or two, 25–180 × 10–20 mm, lanceolate, acute, canaliculate, glaucous, with an undulate and crisped margin, clasping leaf base white, up to 200 mm long. *Inflorescence* subspicate or racemose, dense, many-flowered, 55–130 mm long with a short sterile tip; peduncle erect to suberect, very sturdy, 30–110 mm long, conspicuously inflated below and at base of inflorescence, gradually becoming less inflated towards top of rachis, pale green; pedicels 2–5 mm long; bracts small and membranous, ovate, 1–2 mm long. *Flowers* cernuous to spreading, oblong-campanulate; outer perianth segments ovate-oblong, 6–7 × 3 mm, very pale blue at base, shading to white above, with very large dull red to dark brown gibbositities; inner perianth segments obovate, 8–9 × 3–4 mm, protruding beyond outer segments, white with a greenish brown marking at apex. *Stamens* well exserted, declinate; filaments white, up to 12 mm long. *Ovary* obovate, pale green, 3–4 × 2 mm; style white, up to 9 mm long, protruding beyond stamens as ovary enlarges. *Capsule* obovate, membranous, 8–9 × 5 mm. *Seed* oblong, 2–3 mm long, with a narrow decurrent, inflated terminal arillode 0.2 mm long. Figures 7, 8B & 10.

Etymology: named *L. xerophila* by Schlechter to describe the preference this species has for growing in dry places.

Diagnostic characters

L. xerophila is characterised by a dense subspicate or racemose inflorescence of small oblong-campanulate, white flowers with very large dull red to dark brown gibbositities, and well-exserted, declinate stamens. The sturdy peduncle and rachis are distinctly swollen, and the erect, lanceolate, acute, canaliculate leaf has a distinctly undulate, and sometimes crisped margin. The seed is unique within the genus in having a narrow decurrent, inflated terminal arillode.

L. xerophila is closely related to *L. klinghardtiana* Dinter and *L. physocaulos* W.F.Barker, which fall into the group of species having well exserted stamens and a conspicuously swollen peduncle and rachis. *L. klinghardtiana* also occurs in northwestern Namaqualand, as well as in the Richtersveld and the southwestern corner of Namibia, but differs in having larger oblong-campanulate flowers with much smaller greenish brown to reddish brown gibbositities, borne on a less dense, usually shorter inflorescence. Further, it differs in having a lanceolate-falcate leaf, the peduncle usually has greenish brown blotches or spots, and its seed has a different shape, being globose with an inflated terminal arillode. *L. physocaulos* differs from *L.*

xerophila in having a linear-conducuplicate leaf which widens suddenly into a subterranean clasping base, its flowers are pale magenta and its very small seeds are globose with an inflated terminal arillode. The two species are well separated geographically, as *L. physocaulos* occurs only in the Robertson and Swellendam areas of the southern Western Cape. *Flowering time*: July to September.

Distribution and habitat

Material of this species was first collected by Rudolf Schlechter on 21st September, 1897 at Leeuwpoot just north of Concordia, in Namaqualand. He appended the manuscript name *xerophila* to this material, and distributed it to seven overseas and local herbaria (Barker 1983), where it has languished unpublished for one hundred years. *L. xerophila* is restricted to the dry northwestern and central parts of Namaqualand, and western Bushmanland, where it occurs singly or in colonies in deep red sand in full sun. The fleshy bulb is deep-seated in order to survive the harsh dry summer conditions, and may remain dormant during the winter growth period if rainfall is insufficient. In western Bushmanland, an area of predominantly summer rainfall, *L. xerophila* nevertheless follows the typical pattern of winter rainfall growth and summer dormancy characteristic of the vast majority of species belonging to this genus.

Material examined

NORTHERN CAPE.—2816 (Oranjemund): Holgat, Namaqualand, (–DD), Aug. 1952, *Hall* 558 (NBG). 2917 (Springbok): Leeuwpoot, 14 km N of Concordia, (–DB), Sept. 1897, *Schlechter* 11366 (BM, BOL, G, GRA, K, LD, Z). 2918 (Gamoep): Kennedy's Farm, 40 km E of Springbok, (–CA), Sept. 1967, *Eliovson* 13 (NBG); near Ratelkraal, Namaqualand, (–CA), Sept. 1950, *Barker* 6759 (NBG); Kouberg Farm, off R355 Springbok to Gamoep. Bushmanland, (–CD), Aug. 1972, *Botha s.n. sub. NBG* 95451 (NBG). 3018 (Kamiesberg): Vaalputs Farm, 7 km E of Stofkloof, (–AB), Sept. 1983, *Schelpé s.n. sub. NBG* 127341 (NBG).

ACKNOWLEDGEMENTS

I thank the staff of the Compton Herbarium, Kirstenbosch, especially Dr D.A. Paterson-Jones, Dr J.C. Man-

ning, Mrs J. Beyers and Mrs S.E. Foster for their friendly assistance at various stages of this study. I am also very grateful to Dr O. A. Leistner for kindly preparing the Latin diagnoses, Mrs J. Loedolff for taking the black and white photographs of the herbarium sheets, and Prof. M.C. Botha and Mr R. Symmonds for assistance in the field.

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Studies in the liverwort genus *Fossombronia* (Metzgeriales) from southern Africa. 1. Three new species from Northern Province, Gauteng and Mpumalanga

S.M. PEROLD*

Keywords: *Fossombronia*, Fossombroniaceae, *F. gemmifera* sp. nov., *F. glenii* sp. nov., *F. straussiana* sp. nov., liverworts, Metzgeriales

ABSTRACT

Three new species of *Fossombronia* from Northern Province, Gauteng and Mpumalanga (formerly Transvaal) are described: *F. gemmifera*, *F. glenii* and *F. straussiana*. *F. gemmifera* is distinguished by a highly convoluted pseudoperianth, the frequent presence of gemmae produced dorsally on the stem, lamellate spores and mostly rather short elaters; *F. glenii* can be recognized by a smallish, deeply lobed pseudoperianth, perigonal bracts with finger-like projections shielding the antheridia and by spinous spores; *F. straussiana* is distinct by its hyaline or brownish rhizoids, by its dense, frilly leaves, its pseudoperianth with lamellate lateral outgrowths, by spore ornamentation that usually has inclusions in the incomplete areolae and by the elaters which are finely papillose.

INTRODUCTION

Within the order Metzgeriales the cosmopolitan simple-thalloid liverwort genus *Fossombronia* Raddi is classified in the subfamily Fossombroniaceae Engl. emend. R.M.Schust. (family Fossombroniaceae Hazsl. (= Codoniaceae H.Klinggr.). The Fossombroniaceae is the only family under the suborder Fossombroniineae R.M.Schust. and is regarded as phylogenetically pivotal (Solomon 1995). It comprises four genera: *Petalophyllum* Nees & Gottsche ex Lehm., *Sewardiella* Kashyap, *Austrofossombronia* R.M.Schust. and *Fossombronia*, of which only the latter is known to occur in southern Africa.

Plants of the genus *Fossombronia* are small, usually gregarious with mostly prostrate, fleshy stems, laterally bearing succubously inserted, undulating or crisped thallus wings, dissected into leaf-like segments and free to the base, where they are bistratose, but unistratose elsewhere. The stems are anchored to the substrate by rhizoids which are usually purple, but hyaline in a few rare species.

The gametangia develop acropetally and are situated dorsally along the stem between the leaf insertions. They are either intermingled or borne on separate shoots in monoicous species, or they may occur on separate plants in dioicous species. The antheridia are short-stalked, \pm globose and either naked or shielded by perigonal bracts. The archegonia are exposed, but after fertilization the developing sporophyte becomes surrounded by a campanulate pseudoperianth, constricted at the sometimes stipitate base, and flaring at the plane, lobulate or crisped mouth. The globose capsule is raised on a moderately short or long seta, 6 or 7 to 10 cells in diameter; the capsule wall is bistratose, the outer wall with delicate, hyaline cells and the inner wall with irregularly quadrangular cells, containing nodular and semi-annular thickenings. The walls rupture irregularly into small plates, releasing the spores and

elaters. The spores are relatively large and highly ornamented with spines, lamellae or areolae. The ornamentation on the outer face is generally considered species-specific and regarded as essential for identification, although 'so variable that patterns of ornamentation ... must be used to define taxa' (Schuster 1992). The elaters may be well or occasionally poorly developed and are usually 2- or 3-spiral. The determination of sterile material is extremely difficult, if not impossible because of the plasticity of the gametophytes, the morphology of which varies considerably according to environmental conditions.

HISTORICAL NOTES

The genus *Fossombronia* has been relatively poorly studied in southern Africa. Lehmann (1829) described *Fossombronia* (sub *Jungermannia*) *leucoxantha*, collected by Ecklon on Table Mountain, Devil's Peak and Lion's Head and also reported the presence of *F.* (sub *Jungermannia*) *pusilla* L. on Table Mountain. Gottsche *et al.* (1844–1847) confirmed the presence of *F. pusilla* Nees and described *F. crispa* Nees from Promontorio Bonae Spei. Krauss (1846) reported *F. angulosa* 'in rupibus rivulorum montium natalensium'. Mitten (1878) described *F. tumida* collected by the Rev. A.E. Eaton at the foot of Lion's Head and endorsed the records of *F. crispa* and *F. leucoxantha* from localities near Cape Town. Stephani (1900) described *F. zeyheri* and *F. spinifolia*. Sim (1926) added no new species, but Arnell (1952) described three from the Cape: *F. capensis*, *F. densilamellata* and *F. montaguensis* (Perold 1997: 29). Arnell (1963) stated that 'the South African species of the genus are in great need of revision'. Scott & Pike (1984, 1987a–c, 1988a, b), who studied the genus in Australia (i.e. the western parts of the State of Victoria and adjacent regions of South Australia and New South Wales) for six years and described many new species from there, expected a comparable species richness to emerge from a long-term study of the genus in South Africa (and South America), since they regarded its origins to have been mainly in Gondwanaland.

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MS. received: 1996-06-25.

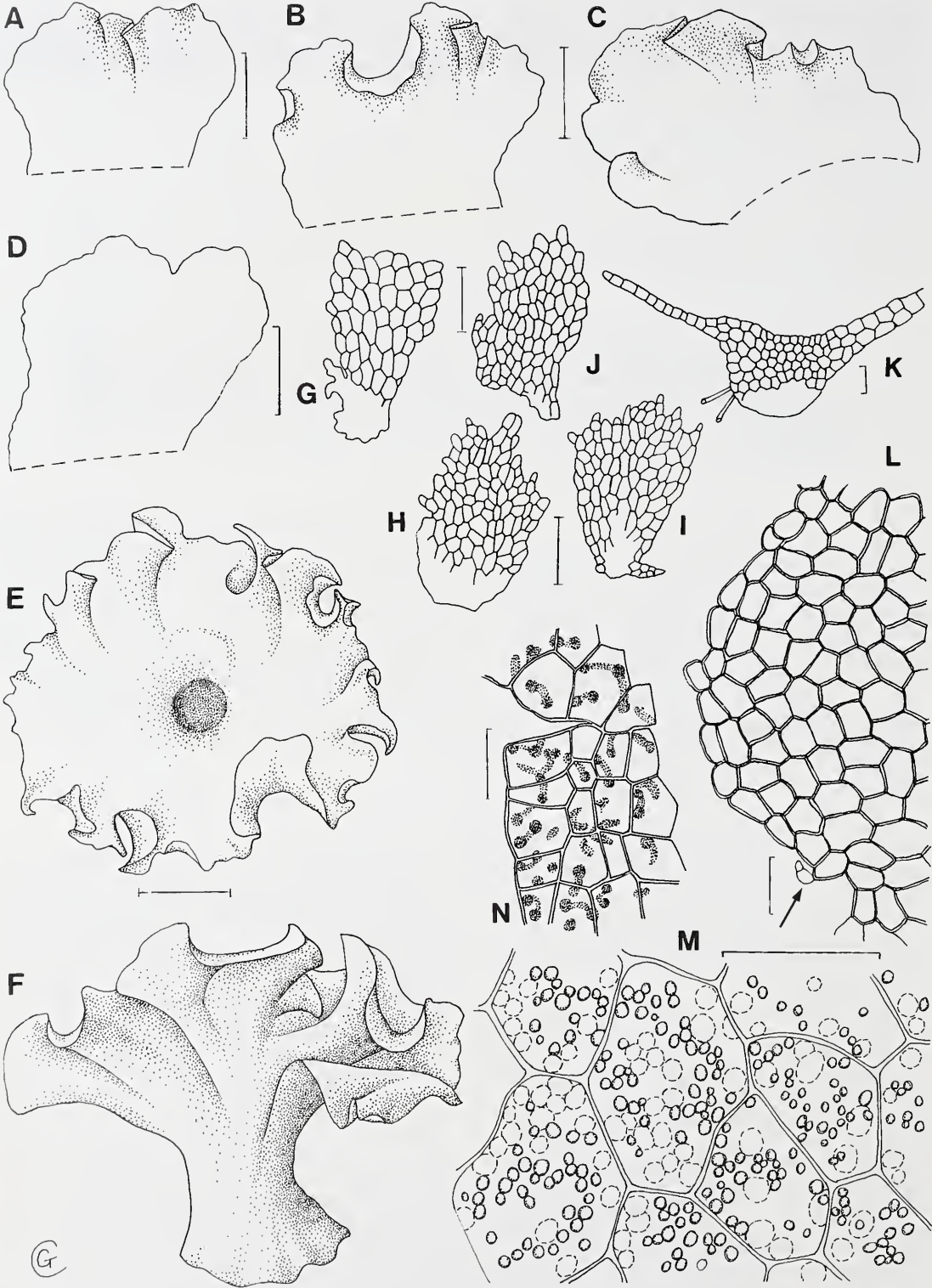


FIGURE 1.—*Fossombronina gemmifera*. A–D, leaves; E, opened pseudoperianth; F, pseudoperianth from side; G–J, perigonal bracts; K, cross section of stem; L, detail of marginal area of leaf, with slime papilla (see arrow); M, median leaf cells with oil bodies and chloroplasts; N, cells in capsule wall. A, D, Strauss & Retief CH13655; B, C, Perold & Koekemoer 3116b; E, F, Perold & Van Rooy 3559a; G–N, Strauss 132. Drawn by G. Condry. Scale bars: A–F, 500 µm; G–J, 250 µm; K, 100 µm; L–N, 50 µm.

This paper is the first of a series dealing with southern African *Fossombronina* species.

METHODS

Samples of field-collected specimens were transferred to a conically shaped fine-mesh sieve and washed in a jet of running water to clear away soil particles. Remaining particles were manually removed by using fine-tipped forceps. Cross sections were cut of some cleaned stems; several leaves and a pseudoperianth were detached and all transferred to a drop of water on a clean slide. Finally a coverslip was applied to the preparation, which was stored in a covered plastic dish lined with damp filter paper. During examination of the slide the evaporated water was periodically replenished. The structures were measured and also photographed under a compound light microscope.

The remaining portion of the cleaned specimen was fixed in FAA (formaldehyde/alcohol/glacial acetic acid and distilled water in proportion of 2:1:1:20). For later reference some thalli were permanently preserved in FAA, the remainder only for several hours and then dehydrated in an ascending series of acetone to 100% and critical point dried in a Balzers Union dryer, using liquid CO₂ as the transitional fluid. The thalli were mounted on aluminium stubs with double-sided Sellotape, gold-coated, then viewed and photographed, using an ISI SX 25 scanning electron microscope (SEM).

There are some advantages to studying and photographing *Fossombronina* material, treated as described above, with the aid of SEM. Scott & Pike (1984) stated that the form, colour and orientation of the leaves (of different species) are distinct but 'beyond our powers to illustrate and exceedingly difficult to describe'. Although the colour cannot be recorded by SEM, the form and certainly the orientation of the leaves can. Scott & Pike (1984) also observed that 'male plants have often shrivelled and disappeared by the time the corresponding spores are ripe and the gametophyte is then so desiccated that its pristine vegetative appearance is irrecoverable'. Samples taken at different stages and treated as above, would have made comparisons easier for them. Scott & Pike did not illustrate the plants of any of their new species, except *F. rudis* (Scott & Pike 1988b) and relied heavily on descriptions and the spore ornamentation to distinguish between species.

The spores and elaters were mounted on slides in Hoyer's fluid for examination and measurement by LM. For SEM microscopy some spores and elaters from the same capsule were allowed to air-dry, mounted on stubs with double-sided Sellotape, gold coated, viewed and photographed. SEM micrographs of *Fossombronina* spores have frequently been published and have been used as an aid to identification. Features of spore morphology should be used with caution, however, because they can be rather variable, and the spores need to be fully mature. The Degree Reference System was used for recording distribution data (Edwards & Leistner 1971).

1. *Fossombronina gemmifera* Perold, sp. nov.

Plantae repentes, gregariae vel dispersae; saepe gemmas dorsaliter secus caulem ferens. *Folia* imbricata, fimbriata, apicem versus aliquando longiora quam latiora, basin versus plerumque breviora quam latiora, nonnulla leviter bilobata, alia apicem versus undulata. *Rhizoidea* purpurea. Monoicae, interdum ut videtur dioicae. *Antheridia* bracteis tecta. *Pseudoperianthium* breviter setatum, orificio intricate convoluto, in lobis multis diviso. *Sporae* 55.0–62.5 µm diametro, superficie distali lamellis minimum 14 irregularibus duplicato-parietatis, aliquando areolas imperfectas facientibus; superficie proximali sine nota triradiata distincta, areolis imperfectis, parietibus altis circumcinctis. *Elateres* 100–160 µm longi, medio 7.5 µm lati, extremitates versus decrecentes, bis vel ter spirales, sed interdum arcte spirales, 50.0–62.5 µm longi, 12.5 µm lati.

TYPE.—Northern Province, 2427 (Thabazimbi): Kransberg, Farm Geelhoutbosch, on streambank, directly south of rondavel, (–BC), *S. Strauss* 132 (PRE, holo.). 2529 (Witbank): ± 80 km E of Pretoria, on Pretoria/Witbank road, facing Balmoral turnoff, left side of road at seepage area, (–CC), *Perold & Van Rooy* 3559a (PRE, para.).

Plants smallish to medium-sized, creeping, gregarious or scattered, green, proximal leaves sometimes clasped around stem, occasionally with pink margins; shoots simple, 5.0–9.0 mm long, 0.85 mm high, 2.6 mm wide, or once/twice furcate, apical segments moderately divergent (Figure 2A) 2.0–5.0 mm long, basally ± 3 mm long. *Stems* prostrate, in cross section apically 300–325 µm (12 or 13 cell rows) high, 400–500 µm wide, basally 250 × 300 µm, plano-convex (Figure 1K). *Rhizoids* purple, 12.5–20.0 µm wide, some with internal mycorrhizal hyphae. *Leaves* overlapping, frilly, obliquely inserted succubously, variously shaped, toward apex sometimes longer than wide, but more proximally usually shorter than wide, 925–1525 × 1325–1625 µm, some slightly bilobed (Figure 1A, D), others rufed above (Figure 1B, C); lateral margins with 3 or 4 uni- or bi-celled slime papillae (Figure 1L). *Leaf cells* thin-walled, at upper margins subquadrate to rectangular across, 32.5–50.0 × 22.5–30.0 µm, at lateral margins long-rectangular, up to 75 × 30 µm; upper laminal cells (4-)5- or 6-sided or polygonal, 32.5–50.0 × 22.5–30.0 µm, middle laminal cells 62.5–72.5 × 37.5–50.0 µm, basal cells 112.5–137.5 × 37.5–62.5 µm. *Oil bodies* glistening, 13–36 per cell, rounded, up to ± 3.5 µm in diameter; chloroplasts numerous, round or oblong, 5.0–7.5 µm in diameter (Figure 1M).

?Monoicous, some specimens with shoots bearing both antheridia and archegonia, but occasionally only antheridia or often only archegonia present. *Antheridia* dorsal on stem, interspersed between archegonia, short-stalked, globose, ± 185 µm in diameter, shielded by an irregularly shaped perigonial bract (Figure 2C), 500–700 × 380–450 µm, margins toothed, with projecting cells and slime papillae (Figure 1G–J), cells in interior 4–6-sided, 80.0–90.0 × 30.0–37.5 µm; sometimes antheridia in groups between leaves and then lacking bracts or with reduced bracts (Figure 2B). *Archegonia* numerous along stem, naked, up to 3 per shoot becoming fertilized, soon

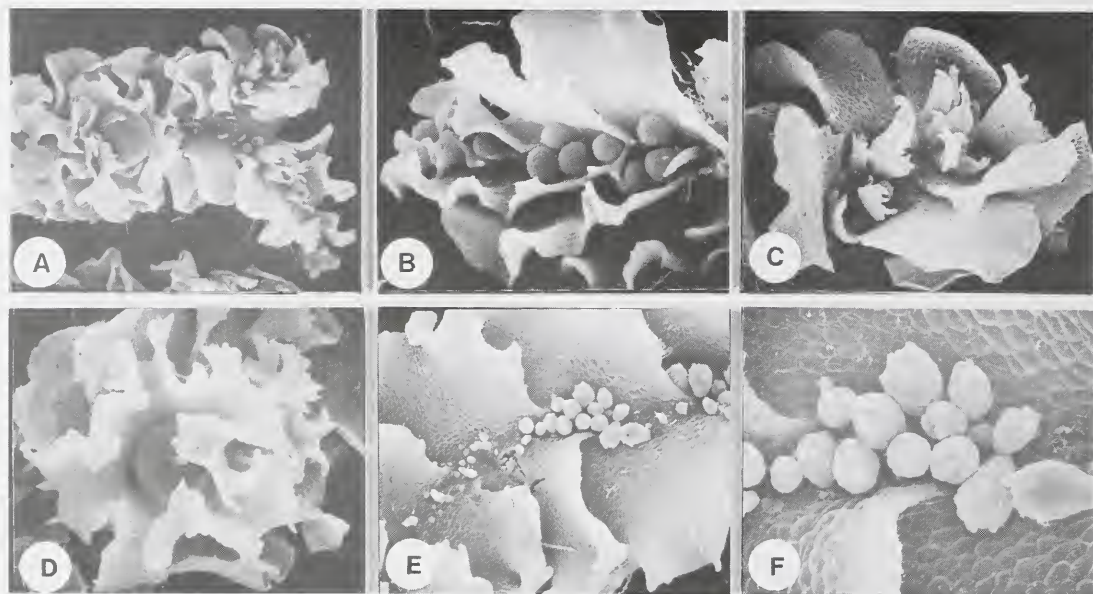


FIGURE 2.—*Fossombronina gemmifera*. A, stem branching near apex, bracts and pseudoperianth with capsule shown, B, antheridia between leaves, C, detail of perigonal bracts with mostly obscured antheridia and young fertilized archegonia; D, convoluted pseudoperianth from above, E, archegonia and gemmae between leaves; F, close-up of gemmae. A, C, D, Strauss 132; B, Perold & Koekemoer 3116b, E, F, Perold & Van Rooy 3557. A, $\times 13$, B, $\times 26$, C, $\times 21$, D, E, $\times 20$, F, $\times 54$.

forming young pseudoperianths. *Pseudoperianths* often crowded together, in acropetal sequence, raised on a short stalk, $\pm 210 \times 470 \mu\text{m}$, widely flaring above (Figure 1F), $\pm 900 \mu\text{m}$ long, up to $2000 \mu\text{m}$ wide across intricately convoluted mouth (Figure 2D), divided into numerous lobes (Figure 1E), $200\text{--}500 \times 150\text{--}440 \mu\text{m}$, some apically rounded, others with an acute apex ending in a papilla; cells comparable in shape and size to those of leaves. *Capsules* globose (Figure 2D), up to $\pm 600 \mu\text{m}$ in diameter, enveloped in a calyptra which is later shed, capsule wall bistratose, cells in inner layer irregularly shaped, $27.5\text{--}50.0 \times 25.0\text{--}37.5 \mu\text{m}$, each cell wall with (1)2–4 nodular and occasionally semi-annular thickenings (Figure 1N). *Seta* delicate, 1.2–3.2 mm long, $270\text{--}350 \mu\text{m}$ in diameter, 6 cells across. *Spores* brown, hemispherical (Figure 3C), $55.0\text{--}62.5 \mu\text{m}$ in diameter, including lamellae projecting around circumference, distal face convex (Figure 3A, B), with at least 14 irregular, mostly double-walled lamellae running across, $\pm 7.5 \mu\text{m}$ apart, occasionally anastomosing and forming incomplete areolae; proximal face (Figure 3D, E) lacking distinct triradiate mark, ornamentation seemingly ‘raised’ from an encircling, marginal furrow (Figure 3E), tall walls forming small, irregular, incomplete areolae, up to $5 \mu\text{m}$ wide, around periphery 19–22 projecting ‘ends’ of lamellae, $\pm 5 \mu\text{m}$ long. *Elaters* (Figure 3F) yellow-brown, smooth, mostly rather small and sometimes poorly formed, $(50.0\text{--})62.5\text{--}85.0 \mu\text{m}$ long, medianly $12.5 \mu\text{m}$ wide, 3(–4)-spiral and loosely coiled, tapering toward tips, $5 \mu\text{m}$ wide and ending in bispiral loops, rarely $100\text{--}160 \mu\text{m}$ long, $7.5 \mu\text{m}$ wide medianly, 3-spiral. *Vegetative reproduction* by gemmae (Figure 2E, F), abundantly borne dorsally along stem, short-stalked, spindle-shaped, up to $300 \times 170 \mu\text{m}$, green when fresh, turning brown with age.

Fossombronina gemmifera grows on sandy loam soil on stream banks or at seepages, often mixed with mosses or

other *Fossombronina* species, particularly *F. straussiana*, which has hyaline rhizoids and is thus easily distinguished from it. This new species is quite distinctive with its highly convoluted pseudoperianth and by the frequent presence of dorsal gemmae for which it has been named. Its spore ornamentation with double-walled lamellae on the distal face and ‘raised’ on the proximal face above a clear marginal furrow, is also unique. There are two other species with purple rhizoids from the same distribution area: *F. glenii* which has spinous spores and *F. zeyheri* which has reticulate spores. *Fossombronina gemmifera* has been collected at several localities in Northern Province and Gauteng (Figure 4).

2. *Fossombronina glenii* Perold, sp. nov.

Plantae repentes, gregariae vel crebrae in coloniis. *Folia* imbricata, undulata, valde obliquiter inserta, plerumque oblonga, longiora quam latiora, apicem versus latiora quam basi, apice subtruncata, lobis vadosis, angulatis. *Rhizoidea* purpurea. Dioicae. *Antheridia* bracteis cum laciniis digitiformibus tecta. *Pseudoperianthium* infundibuliforme, orificio in lobis pluribus diviso, aliquot ad basin divisus. *Sporae* $40.0\text{--}52.5 \mu\text{m}$ diametro, superficie distali cum spinis multis altis conicis, raro fractis vel cristis brevibus junctis; superficie proximali sine nota triradiata distincta, cum tuberculis multis tenuibus vel grossis inspersis. *Elaters* $70.0\text{--}137.5 \times 7.5\text{--}10.0 \mu\text{m}$, bis vel ter spirales.

TYPE.—Northern Province, 2427 (Thabazimbi): Waterberg, Welgevonden Estate, cliffs at drift over Sterkstroom above farmhouse, in partial shade, with *Fissidens erosulus* (Müll.Hal.) Paris, (–BD), *H.F. Glen 2146* (PRE, holo.); *H.F. Glen 2134*, same locality (PRE, para.).

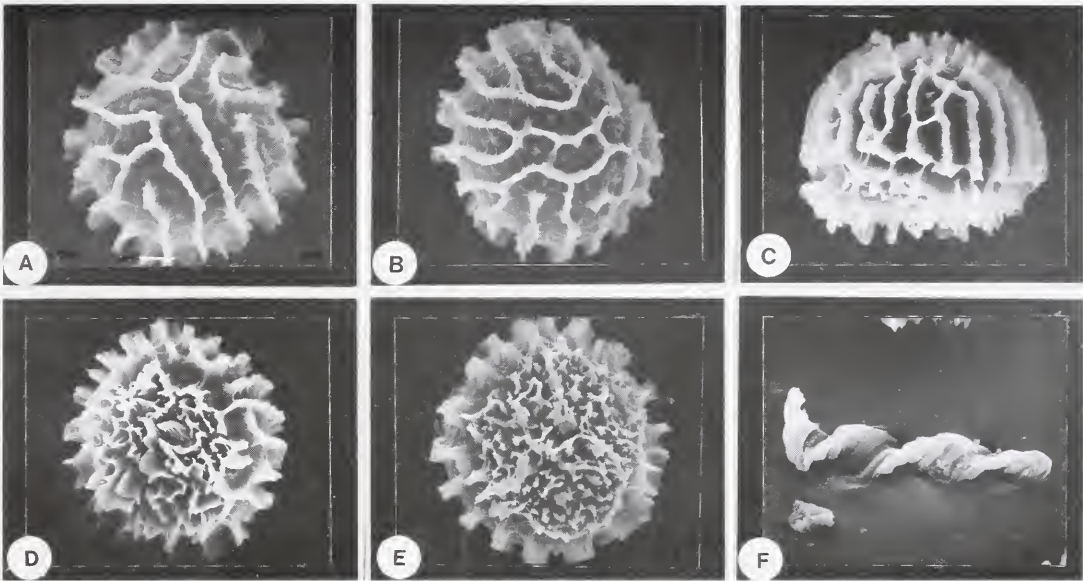


FIGURE 3.—*Fossombronina gemmifera*. Spores and elater. A, B, distal face; C, side view of distal face; D, E, proximal face; F, elater. A, B, D, S.M. Perold 2017; C, E, F, Strauss 132. A, $\times 734$; B, D, $\times 688$; C, E, F, $\times 535$.

Plants medium-sized, creeping, gregarious or in crowded colonies, green; shoots mostly simple, 5.0–7.0 mm long, 1.8 mm high, 3.0 mm wide, occasionally once furcate close to apex (Figure 6A) or to base (Figure 6B), moderately to widely divergent, apical segments 2–5 mm long. *Stems* prostrate, fleshy, in cross section at apex 400–500 μm (13 cell rows) high, 530–650 μm wide, tapering proximally, at base (300–) 400–450 \times 400–480 μm , plano-convex (Figure 5I). *Rhizoids* purple, 12–20 μm wide. *Leaves* overlapping, undulating, very obliquely inserted succubously, generally oblong, longer than wide and wider above than basally, 2000–2500 μm long, width 1325–2500 μm above, 1050–1400 μm below, apex subtruncate, with shallow angular lobes (Figure 5A–F); margins with or without 1 or 2 slime papillae, the lower one on proximal edge of leaf below midline often 2-celled (Figure 5N). *Leaf cells* thin-walled, at upper margins subquadrate, 25–30 \times 32–45 μm , at lateral margins long-rectangular, up to 87.5 \times 22.5 μm ; upper laminal cells 5- or 6-sided, 57.5–75.0 \times 27.5–37.5 μm ; middle laminal cells 62.5–102.5 \times 42.5 \times 47.5 μm ; basal cells 75.0–87.5 \times 37.5–40.0 μm . *Oil bodies* glistening, numerous, more than 50 per cell, up to 2.5 μm in diameter; chloroplasts densely scattered in cells when fresh, but later tending to clump together, $\pm 5 \mu\text{m}$ in diameter (Figure 5O).

Dioicous. *Male plants* hardly smaller than females. *Antheridia* dorsal between leaves, in a row, white when immature, later turning yellow, globose (Figure 6C), short-stalked, $\pm 210 \mu\text{m}$ in diameter, posteriorly shielded by perigonal bracts (Figure 5J–M), $\pm 550 \times 370 \mu\text{m}$, cells in interior subquadrate to hexagonal, 45.0–62.5 \times 40.0–42.5 μm , apices divided into (2)3 or 4 finger-like projections (Figure 6C), 150–300 μm long and 1 or 2 cell rows wide. *Archegonia* naked, in an interrupted, irregular row or in groups dorsally along the stem (Figure 6D). *Pseudoperianths* produced in acropetal sequence, 1 or 2 per shoot, the younger one near the apex and the other

(if present) usually more proximally, but occasionally in close proximity; sessile, \pm funnel-shaped (Figure 5H), at constricted base 425–525 μm wide, up to 1750 μm long, width across flaring mouth 2250–2375 μm , consisting of (4)5 or 6 lobes (Figure 6E), with 1–4(5) deep clefts to near the base (Figure 5G), apices truncate, entire, or with sharply pointed projections; cells comparable in shape and size to those of leaves. *Capsules* globose, $\pm 625 \mu\text{m}$ in diameter, initially entirely enveloped in calyptra, which is later shed, revealing capsule wall (Figure 6F), the latter bistratose, the inner cell layer with irregularly quadrangular cells, 32.5–37.5 \times 20.0–37.5 μm , at each cell wall 2 or 3 nodular and sometimes semi-annular thickenings, (Figure 5P). *Seta* delicate, up to 5.6 mm long, 110 μm in diameter. *Spores* brown, \pm hemispherical (Figure 7D), 40.0–52.5 μm in diameter; distal face convex, usually covered with numerous tall, conical spines up to 5 μm long (Figure 7A), rarely broken (Figure 7B), and

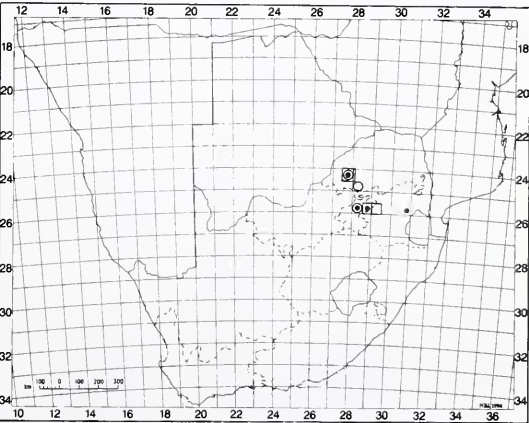


FIGURE 4.—Map showing distribution of *F. gemmifera*, \square , *F. glenii*, \bullet , and *F. straussiana*, \circ , in Northern Province, Gauteng and Mpumalanga.

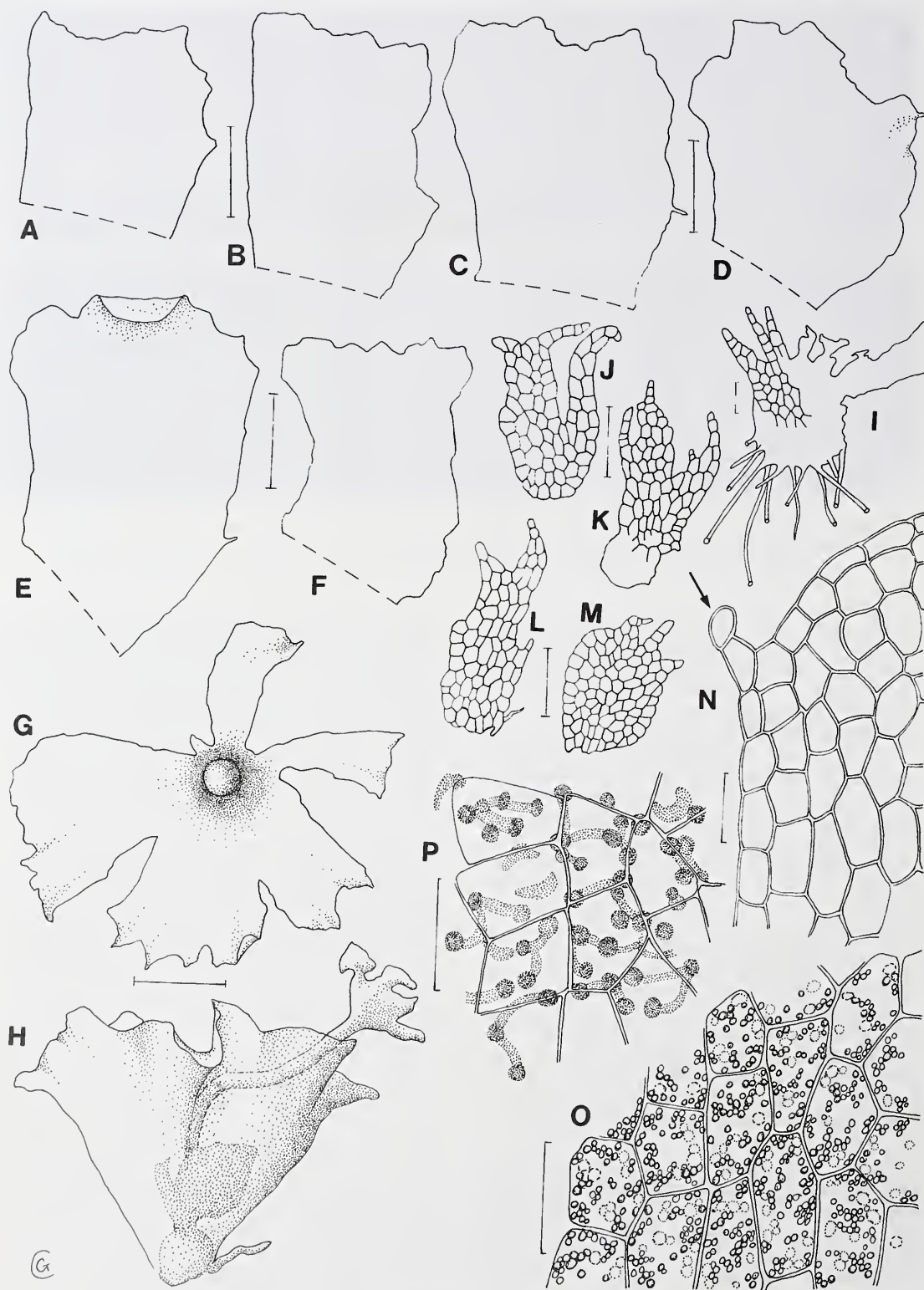


FIGURE 5.—*Fossombronia glenii*. A–F, leaves; G, opened pseudoperianth; H, pseudoperianth from side; I, stem in cross section; J–M, perigonal bracts; N, detail of marginal area of leaf, with slime papilla (see arrow); O, median leaf cells with oil bodies and chloroplasts; P, cells in capsule wall. A–C, E–K, M–P, S.M. Perold 3052; D, L, Glen 2134. Drawings by G. Condry. Scale bars: A–H, 500 µm; J–M, 250 µm; I, 100 µm; N–P, 50 µm.

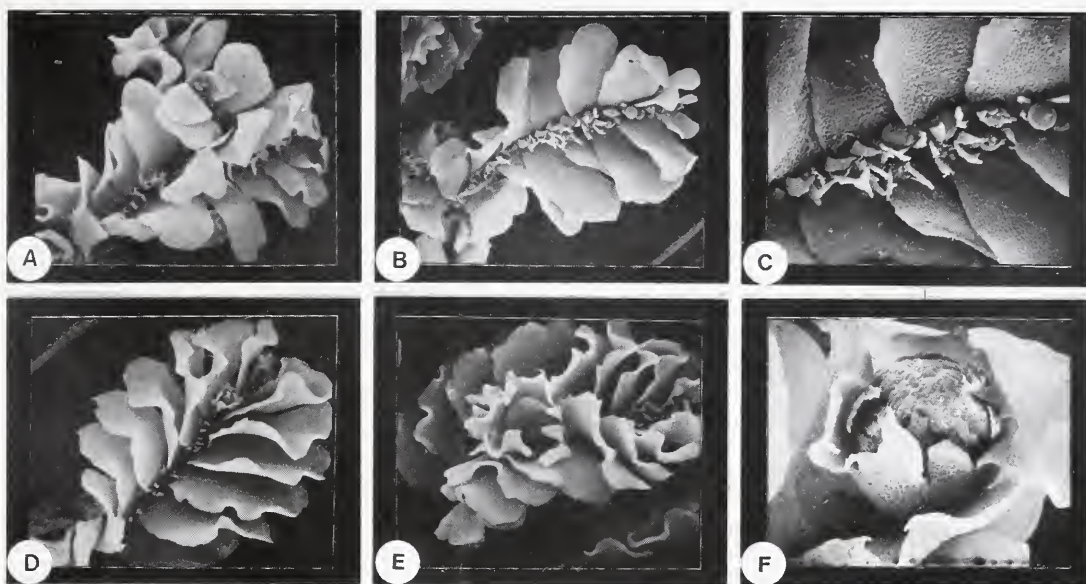


FIGURE 6—*Fossombronía glenii*. A, stem branching near apex, B, stem branching near base; C, antheridia shielded by perigonal bracts, D, archegonia naked along stem, young pseudoperianth near apex, E, pseudoperianth with capsule from above; F, close-up of capsule in pseudoperianth. A, *Perold & Van Rooy* 3569, B–E, *Perold & Van Rooy* 3568, F, *Glen* 2134. A, B, D, E, $\times 7$; C, $\times 15$; F, $\times 23$.

sometimes connected by short ridges, even occasionally forming some high-walled areolae (Figure 7C); proximal face \pm flat, lacking a distinct triradiate mark, sprinkled with numerous fine to coarse tubercles (Figure 7E), which are sometimes rather flattened; circumference with numerous, up to 45, projecting spines. *Elaters* yellow, smooth, 70.0–137.5 μm long, 7.5–10.0 μm wide in middle and tapering slightly toward tips, 2- (Figure 7F) and sometimes 3-spiral in the same elater.

Fossombronía glenii grows on rather sandy soil in dry stream beds or on stream banks, or else on soil pockets in exposed rocky cliffs above streams. So far, it has only been collected at a few localities in Northern Province, Gauteng and Mpumalanga (Figure 4), but it is surely more widespread. It is easily recognized by the rather small pseudoperianth split into several lobes, by perigonal bracts with finger-like projections and by spinous spores. Because of its spinous spores, a specimen collected by *Mogg* (CH

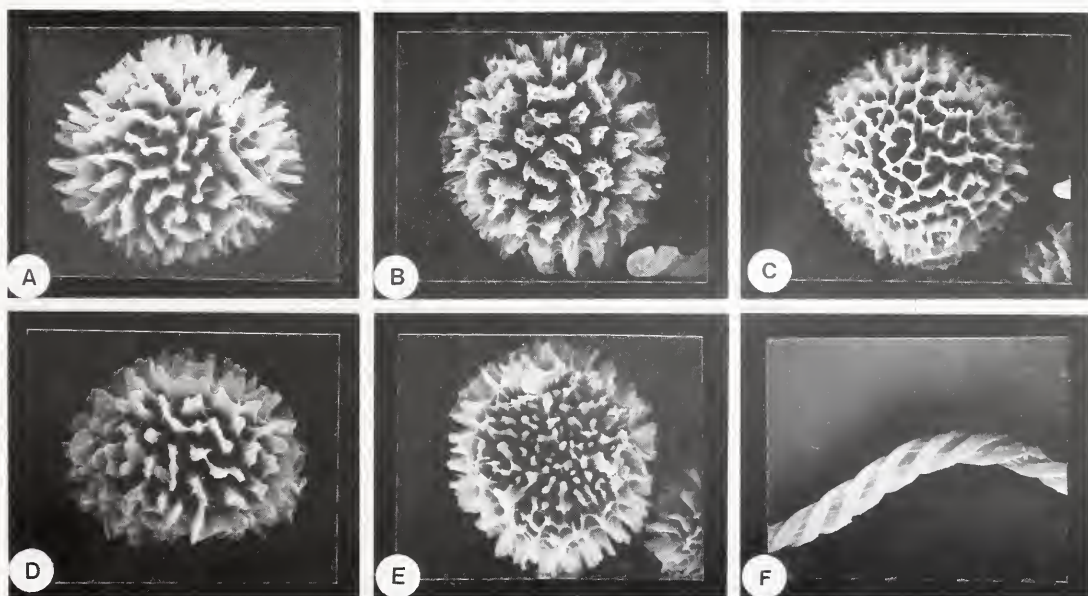


FIGURE 7—*Fossombronía glenii*. Spores and elater. A–C, distal face; D, side view of distal face; E, proximal face, F, elater. A, F, *Glen* 2146, B, D, *Mogg* CH157, C, *S.M. Perold* 3052, E, *Glen* 2134. A, $\times 562$, B, $\times 700$; C, $\times 737$; D, $\times 694$; E, $\times 582$; F, $\times 575$.

157) at Wonderboom Poort, Pretoria, was previously misidentified as the so-called *F. crispa*, but the name had been misapplied (Perold in press). *Fossombronia glenii* is distinguished from the winter rainfall species, *F. leucoxantha*, by the dentate leaves and pseudoperianths (Perold in press). Both species have spinous spores.

This species is named in honour of an esteemed colleague at the National Botanical Institute, Dr H.F. Glen, who has often collected liverworts, together with his wife, Mrs R. Glen (another colleague) and their young daughter, Melissa.

3. *Fossombronia straussiana* Perold, sp. nov.

Plantae repentes, crebrae in coloniis. *Folia* plerumque valde convoluta, dense imbricata, irregulariter formata, longiora vel breviora quam latiora, interdum cum appendiculo oblongo in basi proximali. *Rhizoidea* hyalina vel brunnescentia. Monoicae. *Antheridia* archegoniae conferta, appendiculo foliari basali partialiter circumdata. *Pseudoperianthium* campanulatum, orificio patenti lobati, processibus plures lamellatis lateraliter procurentibus. *Sporae* 35.0–42.5 µm diametro distaliter usque ad 10 lamellis discontinuis, cristis tenuibus interjunctis, aliquando areolas imperfectas facientibus, saepe inclusionibus papilliformibus vel cruciformibus; superficie proximali cum nota triradiata imperfecta, non valde distincta, superficiebus cum papillis humilibus et cristis irregularibus brevibus tectis. *Elaters* 107.5–175.0 µm longi, ter vel bis spirales, papillis tenuibus humilibus tecti.

TYPE.—Northern Province, 2427 (Thabazimbi): Kransberg, Farm Geelhoutbosch, on streambank, directly south of rondavel, (–BC), *S. Strauss* 133 (PRE, holo.); *S. Strauss* 134, same locality (PRE, para.).

Plants medium-sized, creeping, in crowded colonies, green; shoots simple, up to 9.5 mm long, 1.4 mm high, 2.3–3.0 mm wide, or once-furcate, apical segments narrowly divergent (Figure 9A), 4.5–7.5 mm long, basal part 3.0–4.5 mm long. *Stems* prostrate, fleshy, in cross section at apex (300–)400–500 µm (13 cell rows) high, 550–680 µm wide, tapering basally to 300 × 320 µm, plano-convex (Figure 8K). *Rhizoids* of all plants entirely hyaline or brownish, 10.0–12.5 µm wide. *Leaves* mostly highly convoluted, densely imbricate (Figure 9B), obliquely inserted succubously, irregularly shaped, longer than wide (Figure 8B, C) to shorter than wide (Figure 8A, E, F), (575–)1300–1500 × (850–)1025–1500 µm, sometimes with an oblong appendage at proximal base (Figure 8C, D), ± 675 × 500 µm; margins with up to 8 slime papillae at angulations or in between, 22.5–27.5 × 22.5–25.0 µm. *Leaf cells* thin-walled, at upper margins subquadrate or rectangular across (Figure 8L), 25.0–27.5 × 30.0–40.0 µm; at lower lateral margins long-rectangular, up to 47.5 × 22.5 µm; upper laminal cells subquadrate, 25.0–32.5 × 30.0–32.5 µm; middle laminal cells 5- or 6-sided, 47.5–62.5 × 27.5–40.0 µm; basal cells 70.0–75.0 × 50.0 µm. *Oil bodies* glistening, faintly granular, 10–25 per cell, up to 2.5 µm in diameter; chloroplasts densely scattered in cells, 3–5 µm in diameter (Figure 8M).

Monoicous. *Antheridia* short-stalked, globose, 110–135 µm in diameter, dorsal on stem between leaves, basal leaf

appendage partly curved around 1 or 2 (Figure 9D, E), sometimes leaf appendage detached, forming an oblong perigonal bract (Figure 8J), 430–620 × 300–420 µm, margin with 1 or 2 papillae. *Archegonia* in close proximity to antheridia. *Pseudoperianths* soon forming (Figure 9C) after fertilization in acropetal sequence, often 2 per shoot, close together near apex, older more proximal one sometimes with capsule already dehiscent; sessile, campanulate (Figure 9F), at constricted base ± 600 µm wide, 1250 µm, rarely to 1825 µm long, width across flaring mouth 2250 µm, margin ± scalloped, consisting of 4–7 shallow, rounded lobes (Figure 8H), several lamellate outgrowths projecting laterally from sides (Figure 8I); cells comparable in shape and size to those of leaves. *Capsules* globose, 500–610 µm in diameter, capsule wall bistratose, cells in inner layer irregularly shaped, 30.0–37.5 × 15.0–20.0 µm, crowded with nodular and some semi-annular thickenings (Figure 8N). *Seta* 2.25–4.0 mm long, 140–150 µm in diameter, 6 or 7 cells across (Figure 8G). *Spores* light brown, hemispherical (Figure 10B), 35.0–42.5 µm in diameter, including marginally projecting lamellae; distal face convex (Figure 10A, C, D), ornamented with up to 10 discontinuous lamellae, ± 2.5 µm long and 5.0–7.5 µm apart, but interconnected with faint cross ridges, sometimes forming incomplete areolae and frequently with papilla-like or cross-like inclusions; proximal face (Figure 10E) with incomplete and not very distinct triradiate mark, facets covered with low papillae and short irregular ridges, up to 25 lamellae projecting around periphery. *Elaters* light brown, 107.5–175.0 µm long, 7.5 µm wide in middle, tapering to ends, 3-spiral or partly 2-spiral, covered with fine, low papillae (Figure 10F).

Fossombronia straussiana is often mixed with other *Fossombronia* species and grows on streambanks and in seepage areas at several localities in the Northern Province and Gauteng (Figure 4). More specimens of it, *J. Braggins* 91/191 and *S.M. Perold* 2654, were collected in 1991 in Malawi on the Zomba Plateau, as well as at Nyika Nat. Park, *S.M. Perold* 2663; thus it appears to be widespread. Vanden Berghen (1965) reported *F. husnotii* (with hyaline rhizoids) from the Congo Republic, *Symoens* 4329, and from Tanzania (= Tanganyika), *Bryan* 1036. The spores of these specimens have much taller lamellae than those of *F. straussiana* and also appear to differ from those of *F. husnotii*. In 1978 Vanden Berghen reported *F. husnotii* from Shaba, Zaïre (*Malaisse* 9039), without mentioning the rhizoids, but presumably referred here because they are hyaline. Scott & Pike (1988a) comment that the spores of *F. husnotii* are extraordinarily variable and that more research is required. Beside *F. husnotii*, which has mostly hyaline rhizoids, Scott & Pike (1984) also described three new Australian species, *F. punctata*, *F. scrobiculata* and *F. vermiculata*, as having hyaline rhizoids on all or on most plants.

Fossombronia straussiana has been named in honour of Mrs Susan Strauss, owner of the Farm Geelhoutbosch, where she has collected it a number of times, together with other *Fossombronia* species.

This species is easily distinguished by its hyaline or brownish rhizoids and dense, frilly leaves, its pseudoperianth with lamellate, lateral outgrowths, by the spore ornamentation that usually has incomplete areolae with

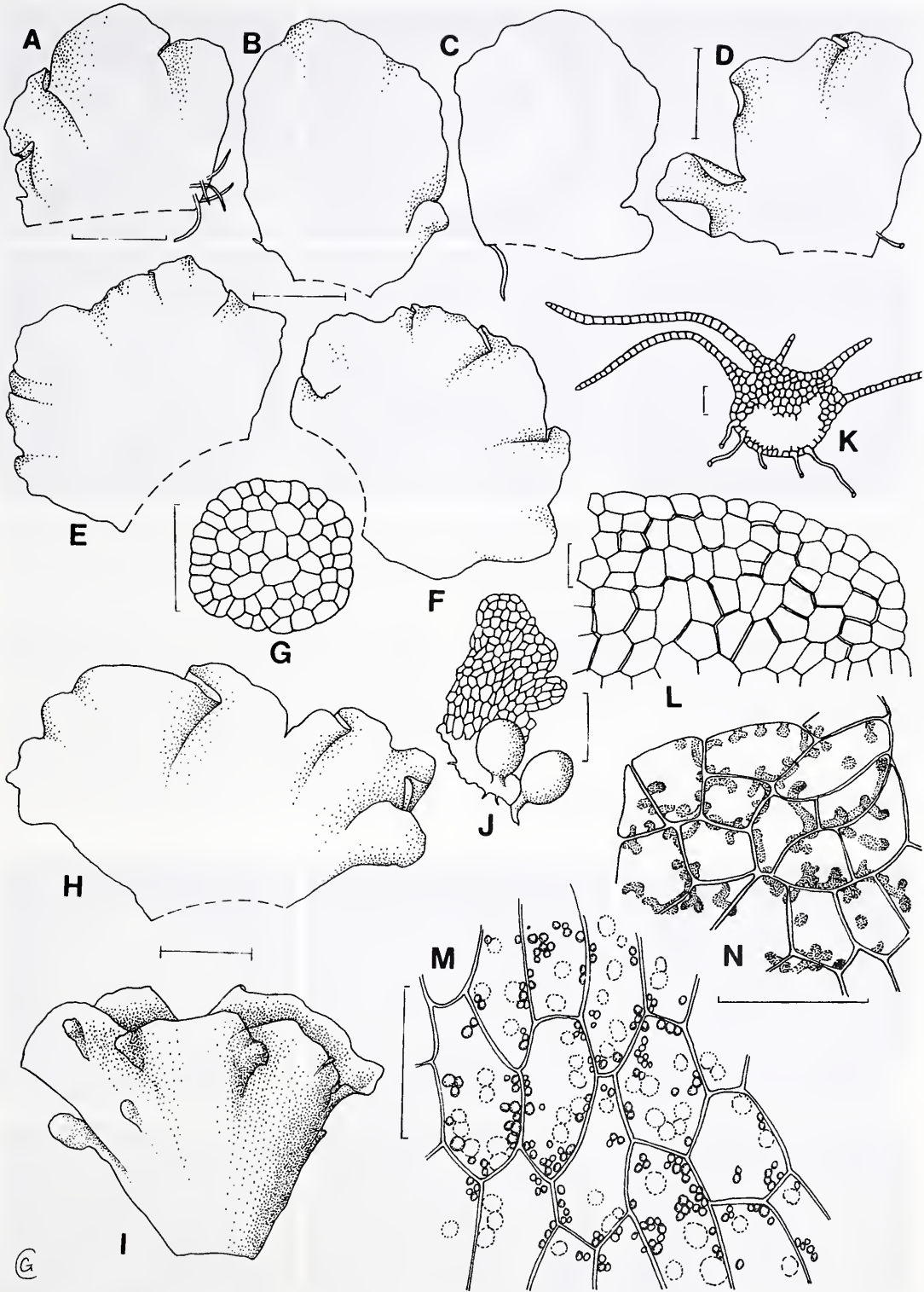


FIGURE 8.—*Fossombronina straussiana*. A–F, leaves; G, cross section of seta; H, opened pseudoperianth; I, pseudoperianth from side; J, perigonal bract and 2 antheridia; K, cross section of stem; L, detail of leaf margin; M, median leaf cells with oil bodies and chloroplasts; N, cells in capsule wall. A–C, E, F, H, I, K, N, *Strauss & Retief CH13655*; D, J, *Perold & Koekemoer 3116a*; G, *Strauss CH13653*; L, M, *Strauss CH13651*. Drawings by G. Condy. Scale bars: A–F, H, I, 500 µm; G, K, 100 µm; J, 250 µm; L–N, 50 µm.

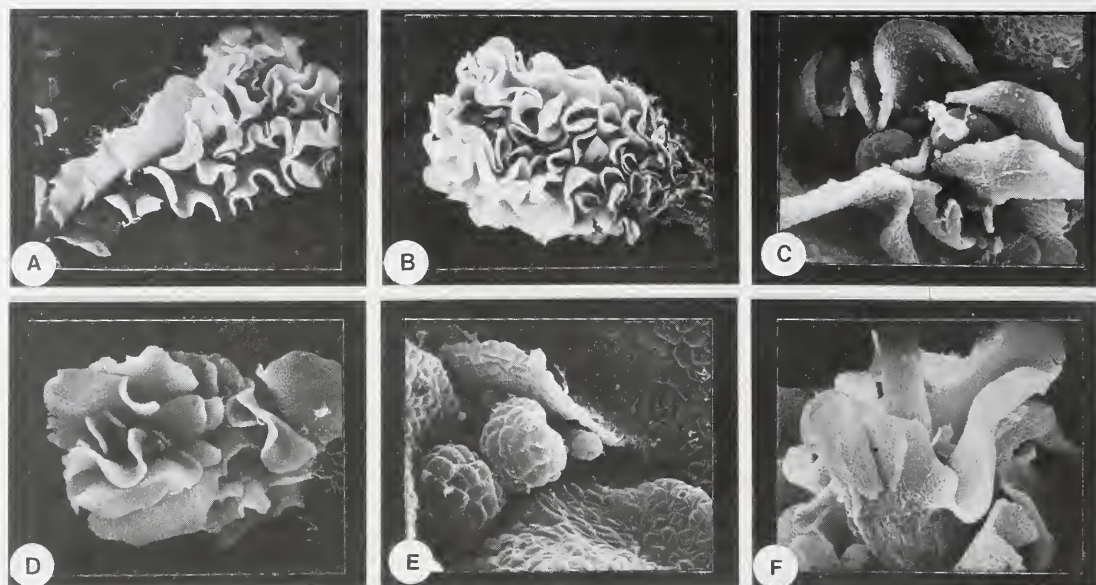


FIGURE 9.—*Fossombronina straussiana*. A, stem branching near apex; B, leaves crowded on stem; C, antheridium and archegonium in close proximity between leaves; D, proximal leaf appendage curved around gametangia; E, close-up of same; F, pseudoperianth with seta emerging from it. A, F, Strauss 133; B, Perold & Koekemoer 3124a; C–E, Perold & Koekemoer 3116a. A, $\times 7$; B, $\times 10$; C, $\times 66$; D, $\times 15$; E, $\times 106$; F, $\times 23$.

inclusions and by the usually finely papillose elaters. The specimen, *Scott 13*, has a larger and more elaborate pseudoperianth than those usually encountered in this species. Its spore ornamentation is very similar, however, and the rhizoids are hyaline.

ACKNOWLEDGEMENTS

I wish to thank the referees of this article, Dr E.O. Campbell and Prof. R. Stottler for their constructive com-

ments as well as the kind people who have collected specimens for me, particularly Dr H.F. Glen and Mrs Susan Strauss, also my colleagues at the National Botanical Institute, Ms Marinda Koekemoer and Mr Jacques van Rooy who helped me with fieldwork. Many thanks to Dr Glen for translating the diagnoses into Latin, Mrs J. Mulvenna and Ms D. Maree for typing the manuscript, Ms G. Condy for the drawings and Mrs A. Romanowski for developing and printing many photographs.

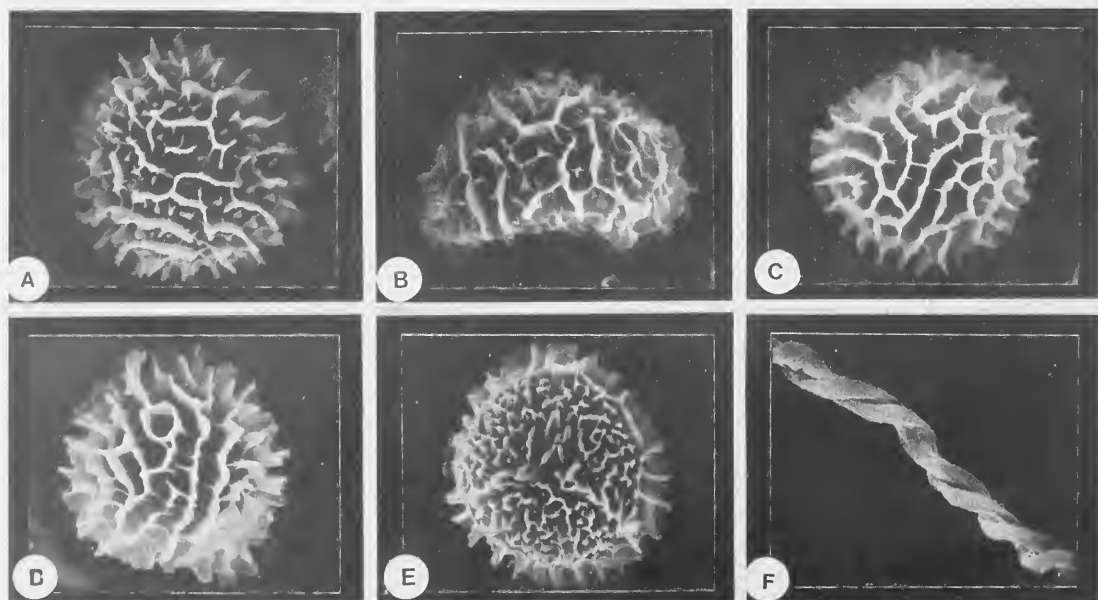


FIGURE 10.—*Fossombronina straussiana*. Spores and elater. A, C, D, distal face; B, side view of distal face; E, proximal face; F, elater. A, B, E, *Scott 13*; C, *Strauss & Retief CH13655*; D, *S.M. Perold 3280*; F, *Perold & Koekemoer 3124a*. A, C, $\times 727$; B, $\times 1084$; D, $\times 588$; E, $\times 674$; F, $\times 839$.

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SPECIMENS EXAMINED

Held at PRE, unless otherwise indicated. Bracketed numbers after citation of collector's name and collecting number refer to the species described in the text in alphabetical order, namely: *F. gemmifera* (1); *F. glenii* (2); and *F. straussiana* (3).

Braggins 91/191 (3) (Malawi).

Glen 2134 (2) (paratype), 2146 (2) (holotype).

Koekemoer 976 (2).

Mogg CH157 (2) BOL, PRE.

Perold S.M. 2017 (1); 3052 (2); 3280, 3281, 2654 (Malawi), 2663 (Malawi) (3). Perold & Koekemoer 3116a, 3124a (3); 3116b, 3124b, 3129 (1). Perold & Van Rooy 3555, 3559a (paratype), 3564, 3565 (1); 3568, 3569 (2).

Scott 13 (3) CH3697. Strauss 132 (1) (holotype), 133 (3) (holotype), 134 (3) (paratype), CH13651, CH13653, CH13654 (3). Strauss & Retief CH13655 (3).

Wager 14 (3).

Studies in the liverwort genus *Fossombronina* (Metzgeriales) from southern Africa. 2. An amendment to three species from Western Cape, described by S.W. Arnell

S.M. PEROLD*

Keywords: *Fossombronina*, *F. capensis*, *F. densilamellata*, *F. montaguensis*, Hepaticae, Metzgeriales, southern Africa, Western Cape

ABSTRACT

Subsequent to his visit to South Africa in 1951, S.W. Arnell (1952), described three new *Fossombronina* species from Western Cape, namely *F. capensis*, *F. densilamellata* and *F. montaguensis*. Unfortunately, however, they were not described in detail, nor were they fully illustrated. An attempt is hereby made to augment Arnell's descriptions and to illustrate his species more completely, with the aid of drawings and SEM micrographs. A distribution map is also provided. Scott & Pike (1988), after examining many *Fossombronina* specimens of world-wide origin, concluded that the above three species were good species, a conclusion I support.

1. ***Fossombronina capensis*** S.W. Arnell in Botaniska Notiser 3: 314 (1952); S.W. Arnell: 81 (1963). Type: Western Cape, 3423 (Knysna): Bracken Hill Forest, (–AA), roadside, S.W. Arnell 1376 (S, holo.; PRE, iso.).

Plants in crowded colonies, green; shoots medium-sized in male plants, 10–15 mm long, 1.3–2.0 mm high, 2.8–3.0 mm wide; female plants more common and rather larger, simple, up to 18 mm long, 1.5–2.5 mm high, 2.5–4.0 mm wide, or once/twice to repeatedly furcate, segments moderately to widely divergent, 4.0–6.0 mm long. *Stems* prostrate, tapering proximally, chlorophyllose, occasionally ventral row of cells purple, sometimes with a lateral bud or side branch, plano-convex in cross section, in male plants (Figure 1I) 250–350 µm (11 cell rows) high, 420–610 µm wide, in female plants (Figure 1J) 270–350 µm (10–12 cell rows) high, 400–610 µm wide. *Rhizoids* purple, ± 15 µm wide. *Leaves* overlapping, widely spreading, succubously inserted (Figure 2A), apically small, free margin rounded, soon becoming larger, obovate, short- or long-rectangular, or irregularly shaped, occasionally slightly notched and shortly bilobed; in male plants rather smaller (Figure 1A–D), 1125–1375 × 1225–1350 µm; in female plants (Figure 1E–G) mostly larger, 1000–2750 × 1150–2575 µm above, sometimes, when sides not parallel, narrower below, 1075–1750 µm wide; margins almost entire or with ± 6 well-spaced slime papillae, ± 25.0 × 17.5 µm. *Leaf cells* thin-walled, in male plants not appreciably different from those of females, at upper margins (Figure 1H) rectangular across, 22.5–32.5 × 37.5–45.0 µm, at lateral margins long-rectangular, 40.0–62.5 × 20.0–25.0 µm, upper laminal cells 5- or 6-sided, 37.5–57.5 × 35.0–50.0 µm, middle laminal cells (Figure 1K) 65.0–87.5 × 50.0–57.5 µm, basal cells 67.5–87.5 × 50.0–62.5 µm. *Oil bodies* quite variable in number, 17–37 per cell, larger ones ± 5 µm in diameter and granular, others much smaller and smooth; chloro-

plasts numerous, mostly rounded, ± 5 µm in diameter, sometimes elongate, 7.5 µm long (Figure 1K).

Dioicous. *Antheridia* dorsal on stem, generally in 2 crowded rows (Figure 2B), short-stalked, globose or ovoid, 160–250 µm in diameter, each shielded by a bract (Figure 1M–P), 480–770 × 330–640 µm, sometimes 2 adjacent ones joined together, margins with 3 or 4 projecting papillae or processes, cells in interior 4- or 5-sided, 42.5–75.0 × 37.5–67.5 µm. *Archegonia* in 1 or 2 rows (Figure 2C, D) along stem, naked; sometimes several per branch, at intervals (Figure 2E) or 2 adjacent, becoming fertilized. *Pseudoperianth* (Figure 1Q, R) campanulate, proximal to apex, as tall as leaves or projecting somewhat above them, raised on a short stalk, then widely flaring above, 1875–2125 µm long, 1625–2125 µm wide across mouth, margin with 10–15 angular projections, each with a papilla, ± 20.0 × 17.5 µm, often with winged outgrowths on outside (Figure 2F); cells comparable in shape and size to those of leaves. *Capsules* globose, ± 850 µm in diameter, wall bistratose, cells in inner layer irregularly shaped (Figure 1T), 32.5–50.0 × 27.5–35.0 µm, each cell wall with 1–3 dark brown, nodular and sometimes semi-annular thickenings. *Seta* 2.8–4.0 mm long, 250–300 µm in diameter, 6–8 cells across (Figure 1L). *Spores* golden brown to brown, hemispherical, 42.5–55.0 µm in diameter, including lamellae projecting at margin; distal face (Figure 3A, B) convex, with up to 8 lamellae, ± 5 µm high and 5–10 µm apart running across face, sometimes in different directions or parallel to each other (Figure 3C), occasionally anastomosing and forming a few to several areolae, surface between lamellae with fine cross striations (Figure 3D); proximal face (Figure 3E) lacking triradiate mark, flat, covered with irregularly shaped papillae and short ridges, sometimes with scattered granules, 12–16 'spines' (i.e. 'end-on' view of terminations of lamellae from the distal face) projecting around spore periphery and joined by a 5 µm wide, incomplete membranous wing or perispore. *Elaters* (Figure 1S) mostly delicate, outer wall collapsing on drying, rather short and stout, blunt at tips, 62.5–125.0 × 10.0–12.5 µm, loose spirals faintly greenish yellow, strands often difficult to distinguish, but

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MS. received: 1996-10-08.

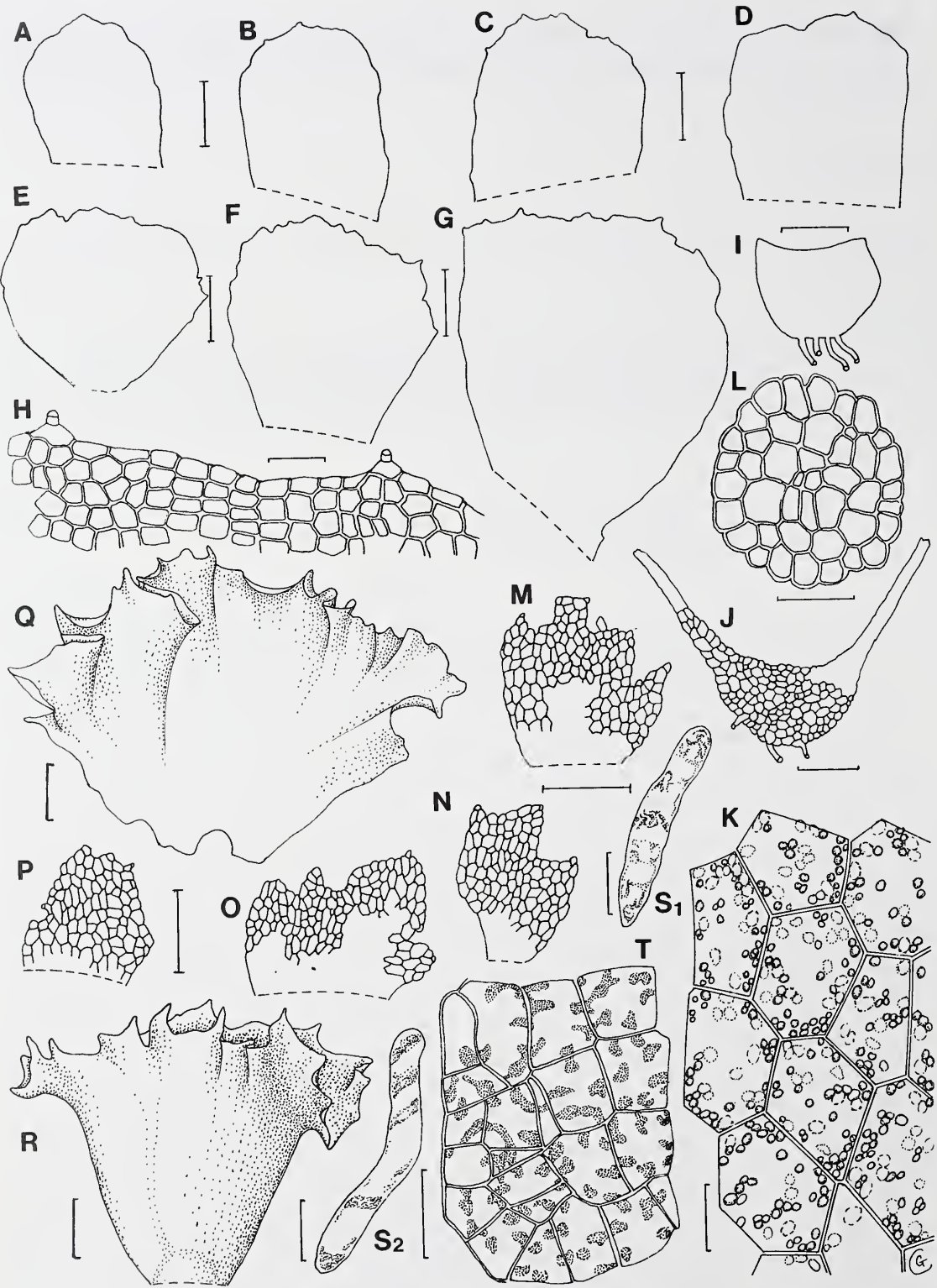


FIGURE 1.—*Fossombronina capensis*. A–D, male leaves; E–G, female leaves; H, detail of upper margin of leaf; I, cross section of male stem; J, cross section of female stem; K, median leaf cells with oil bodies (solid lines) and chloroplasts (dotted lines); L, cross section of seta; M–P, bracts; Q, opened pseudoperianth; R, pseudoperianth from side; S₁, S₂, elaters; T, cells in capsule wall. A, B, *Koekemoer* 998; C–K, M–R, *S.M. Perold* 3494; L, S, T, *S.M. Perold* 3492. Scale bars: A–G, Q, R, 500 µm; I, J, M–P, 250 µm; L, 100 µm; H, K, T, 50 µm; S₁, S₂, 25 µm.

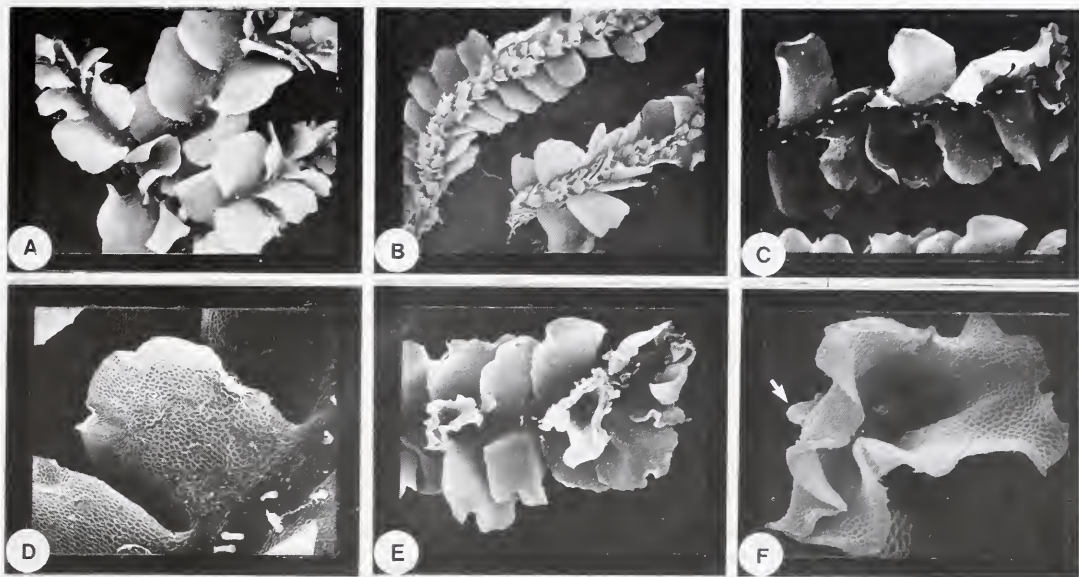


FIGURE 2.—*Fossombronia capensis*. A, thallus branches; B, male plants with rows of bracts; C, female plant with 1 or 2 rows of archegonia; D, detail of female plant with archegonia; E, female plant with 2 pseudoperianths; F, young pseudoperianth from above with outgrowth (see arrow). A, S.M. Perold 3497; B–F, Koekemoer 998. A, B, C, E, $\times 7$; D, F, $\times 30$.

sometimes better developed, with brown rings or even 3 spirals and narrowed at tips, 5 μm wide (Figure 3F).

The correct collector's number of the holotype specimen is Arnell 1376 and not 1876 (Arnell 1952). *Fossombronia capensis* is confined to the southeastern Western Cape, in the winter rainfall region (Figure 4). It grows on

soil, rarely extending onto slate, in forests, at roadsides, or in clearings, on streambanks or on vertical, shaded rock walls in soil pockets. It is distinguished by the relatively large size of the female plants with overlapping leaves and exposed stems, by fairly common, smaller male plants with large bracts subtending 2 rows of adjacent antheridia, by the spore ornamentation with widely separated lamellae and marginally by 12–16 projecting 'spines' joined by

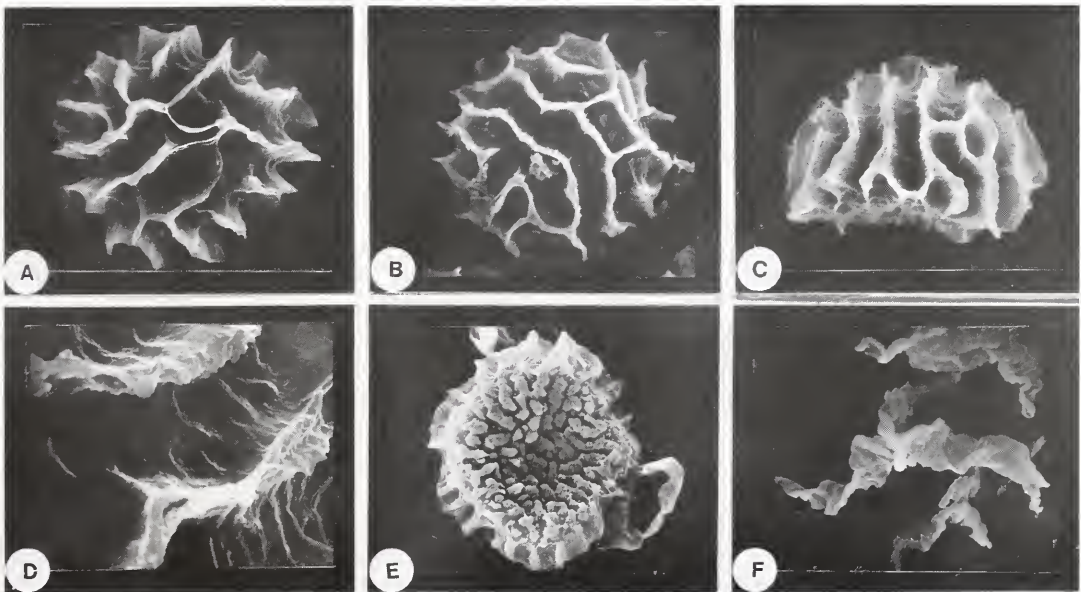


FIGURE 3.—*Fossombronia capensis*. Spores. A, B, distal face; C, side view of distal face; D, detail of lamellae and spore surface on distal face; E, proximal face; F, elaters. A, Arnell 1783; B, Arnell 1555; C, S.M. Perold 3494; D, Arnell 1470; E, Koekemoer 998; F, Arnell 1477. A, $\times 612$; B, $\times 672$; C, $\times 625$; D, $\times 2755$; E, $\times 739$; F, $\times 406$.

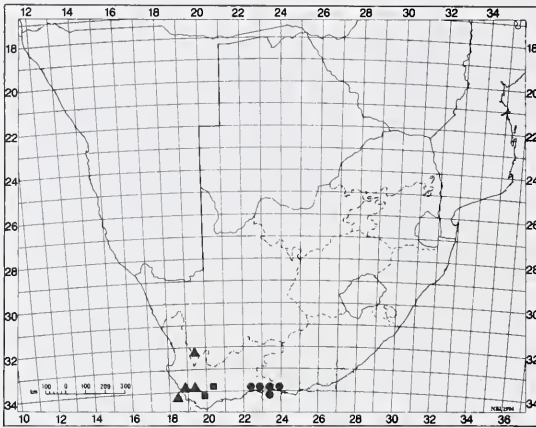


FIGURE 4.—The distribution of *Fossombronia capensis*, ●; *F. densilamellata*, ▲; and *F. montaguensis*, ■, in southern Africa.

an incomplete membranous wing or perispore and also by generally reduced, delicate elaters. Arnell (1952, 1963) referred to the latter as 'leaf-like'. Poorly formed elaters are also present in *F. cristula* (Piippo 1991; Scott & Pike 1987) and in *F. foveolata* var. *cristula* (Schuster 1992). Schuster treated *cristula* as a variety of *F. foveolata*, although it is regarded by Scott & Pike (1987) as a complex [in which they include the southern African *F. zeyheri* (Perold in press)]. According to Scott & Pike (1987), curious and variously malformed elaters are quite common and they found *cristula*-type elaters occurring in individuals apparently belonging to a number of other taxa, with spores unlike those of the *F. foveolata* complex. They admit, however, that *F. cristula* and *F. foveolata* are perhaps not distinct, but on the evidence of dioicism versus monoicism, they presently maintain them as separate species. All *F. capensis* specimens are dioicous and those from the George/Knysna/Brackenfell/Gouba and Deep Walls Forests and Diep River areas have poorly formed elaters. Collections from the nearby Bloukranz Pass (*Liibena-Nestlé* SA 139/2 and *S.M. Perold* 3534, 3539–3541) have elaters with well-formed spirals, but have been referred here because the spores and plants are closely similar.

The strong aromatic smell referred to by Arnell was not observed. Arnell (1952) stated that the spores of *F. capensis* and *F. pusilla* had the same appearance, but he distinguished *F. capensis* from the latter because it was dioicous and had large bracts subtending the antheridia in the male plants. Initially Arnell (1953) thought that *F. pusilla* did not grow in South Africa, but in his *Hepaticae of South Africa* (Arnell 1963) he included it. Its presence here still needs to be confirmed. Earlier reports of it (Lehmann 1829; Gottsche *et al.* 1846; Sim 1926) are most probably based on misidentifications. Best (1990) lists *F. pusilla* as present in Zimbabwe. Vána *et al.* (1979) reported the presence of *F. capensis* and *F. pusilla* in Rwanda and Burundi, but they doubted the determination of *F. capensis* for a specimen from Rwanda. Examination of the spores of *De Sloover* 18574 (BR) from Rwanda shows it to belong to a different species. *De Sloover* 13.345 and 19.118 are sterile. *F. capensis* appears to be confined to a relatively small area in the southeastern part of Western Cape which has winter rainfall. Its spores ripen in spring and summer.

2. *Fossombronia densilamellata* S.W.Arnell in Botaniska Notiser 1952: 317 (1952); S.W.Arnell: 80 (1963). Type: Western Cape, 3318 (Cape Town): Lion's Head near Kloofnek, (–CD), S.W. Arnell 295 (S, lecto., here designated; PRE, isolecto.).

Plants in dense colonies or overlying mats, pale green to yellow-green, older leaves dying, turning yellow-brown and translucent, lower part of stem occasionally almost denuded of leaves; shoots smallish to medium-sized in male plants, up to 12 mm long, 1.1 mm high, 2.5 mm wide; female plants far more common and rather larger, shoots sometimes simple, 9–14 mm long, 1.4–1.7 mm high, 1.6–3.8 mm wide, at pseudoperianth up to 4.4 mm wide, mostly bifurcate with terminal segments (Figure 6A) closely to moderately divergent and of unequal length, 2–4 mm long. *Stems* prostrate, green, occasionally central core purple, sometimes apically very shortly branched, with dorsal bud-like layers of small leaves at tips, lateral branches often developing from latero-ventral buds, plano-convex in cross section, in male plants (Figure 5I) apically 210 µm (9 cell rows) high, 400 µm wide, basally 350 µm high, 350 µm wide, in female plants apically swollen (Figure 5J), 460 µm (± 16 cell rows) high, 700 µm wide, gradually tapering toward base (Figure 5K), 280 µm high, 430 µm wide. *Rhizoids* purple, 12.5–20.0 µm wide, sometimes with flat tips. *Leaves* erect, imbricate, undulate along upper margin, succubously inserted, markedly decurrent on stem (Figure 6B), subquadrate to rectangular, sometimes wider above than below, apex truncate or with several low triangular or toothed projections, in male plants (Figure 5A–C) 1125–1750 × 1125–1625 µm, in female plants mostly larger (Figure 5D–G), 1625–2750 µm long, width above 1250–2125 µm, below 825–1250 µm; margins with up to 13 slime papillae, 25.0 × 22.5 µm, mostly at angulations and often more numerous on distal (leading) edge (Figure 5C) than on proximal (trailing) edge. *Leaf cells* (Figure 5H) above somewhat thicker-walled than below, in male plants not appreciably different from those of females, at upper margins rectangular across, 27.5–35.0 × 32.5–57.5 µm, at lateral margins long-rectangular, 52.5–75.0 × 20.0–22.5 µm, mostly longer at proximal edge, up to 140.0 × 17.5 µm, upper laminal cells 4- or 5-sided, 45–50 × 45–50 µm, middle laminal cells 6- or 7- sided, walls bulging, 82.5–95.0 × 50.0–55.0 µm, basal cells 100–125 × 25–60 µm. *Oil bodies* (Figure 5L) very variable in number, in young leaves some cells with 8–10, in others much more numerous, round or bean-shaped, up to 2 µm in diameter; chloroplasts numerous, rounded, ± 5 µm in diameter.

Dioicous. *Antheridia* dorsal on stem, in 1 or 2 rows, globose, ± 180 µm in diameter, each shielded by a bract (Figures 5M–O; 6C), 300–450 × 320–400 µm, with several projections, mostly topped by a mucilage papilla, cells in body 4–7-sided, ± 62.5 × 25.0 µm. *Archegonia* (Figure 6D) in a row dorsally along stem, naked, sometimes several per branch becoming fertilized, occasionally next to each other or even surrounded by the same pseudoperianth. *Pseudoperianth* (Figures 5P, Q; 6F) campanulate, proximal to apex (Figure 6E), projecting ± 750 µm above top of leaves, raised on a short stalk, ± 425 × 500–700 µm, then widely flaring above, 2250–2750 µm long, 2375 µm wide across mouth, its margin with toothed or angular projections, 200–250 µm long, crowned with papillae,

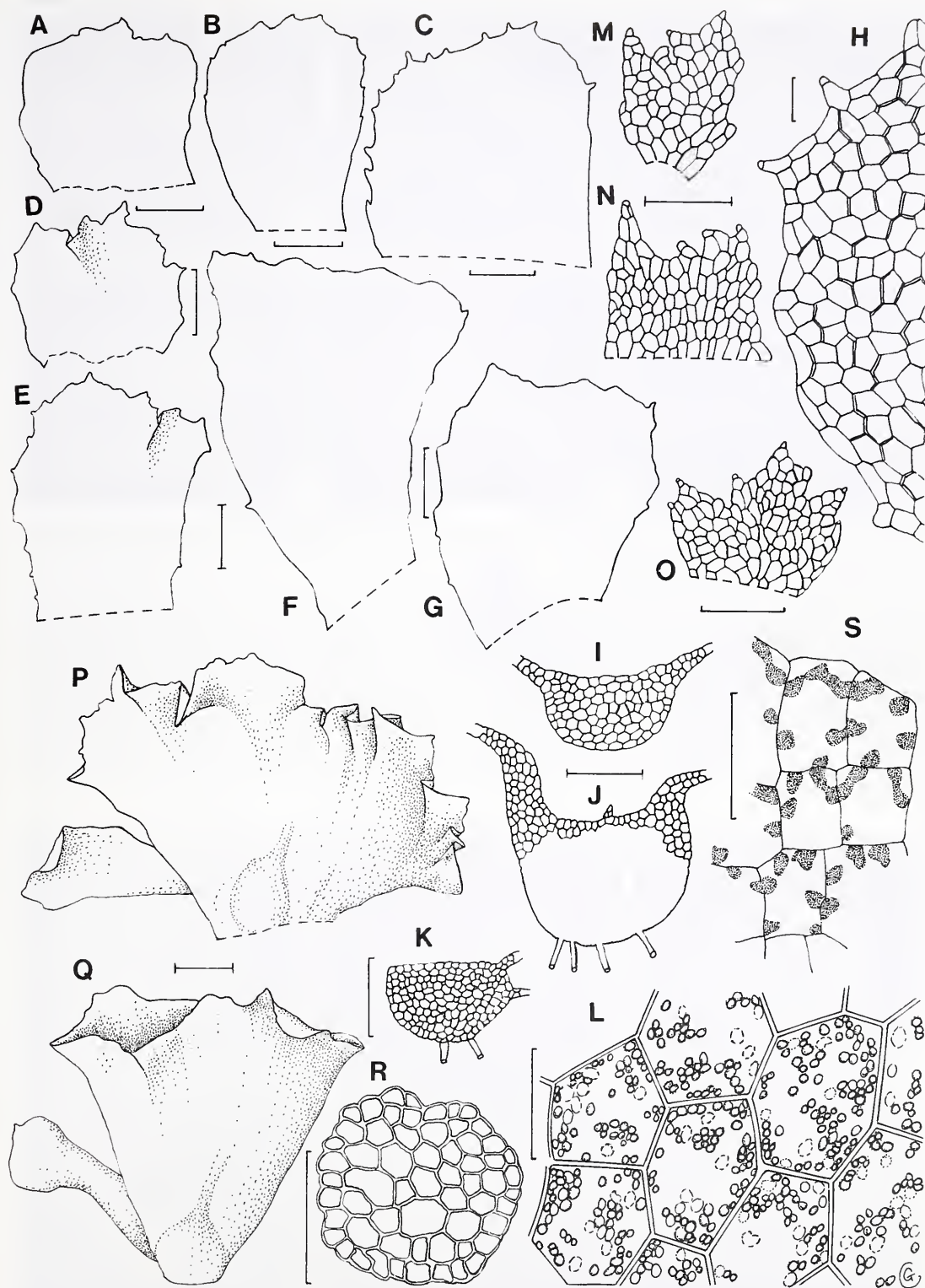


FIGURE 5.—*Fossombronina densilamellata*. A–C, male leaves; D–G, female leaves; H, detail of distal margin of male leaf; I, cross section of male stem; J, cross section of apical part of female stem; K, cross section of basal part of female stem; L, median leaf cells with oil bodies and chloroplasts; M–O, bracts; P, opened pseudoperianth; Q, pseudoperianth from side; R, cross section of seta; S, cells in capsule wall. A, B, E–G, I–K, M, O, P–S, *S.M. Perold* 3349; C, H, N, *Garside* 6510; D, L, *S.M. Perold* 629. Scale bars: A–G, P, Q, 500 µm; H, R, 100 µm; I–L, S, 50 µm; M–O, 250 µm.

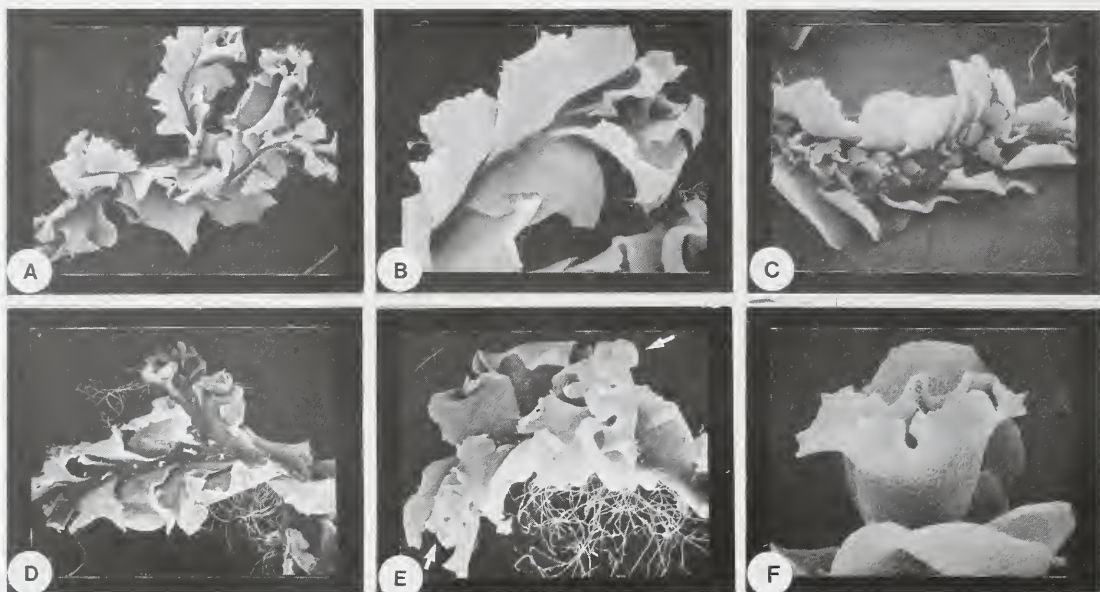


FIGURE 6.—*Fossombronía densilamellata*. A, thallus branches; B, apical leaves; C, male plant with rows of bracts; D, female plant with row of archegonia; E, female plant with 2 pseudoperianths (see arrows); F, pseudoperianth. A–C, *S.M. Perold 3346*; D–F, *S.M. Perold 3349*. A, D, $\times 7$; B, $\times 17$; C, $\times 13$; E, $\times 9$; F, $\times 20$.

$\pm 22.5 \times 17.5 \mu\text{m}$, sometimes with a winged outgrowth at the side, $\pm 1925 \mu\text{m}$ long, $775 \mu\text{m}$ wide at apex; cells comparable in shape and size to those of leaves. *Capsules* globose, $700\text{--}875 \mu\text{m}$ in diameter, cells in inner layer of bistratose wall (Figure 5S) irregularly shaped, $35.0\text{--}50.0 \times 27.5\text{--}37.5 \mu\text{m}$, each cell wall with 2 or 3 nodular and sometimes semi-annular thickenings. *Seta* (Figure 5R) $5.0\text{--}9.5 \text{ mm}$ long, $140\text{--}150 \mu\text{m}$ in diameter, up to 8 cells across. *Spores* light brown or yellow-brown, hemispheri-

cal, $40\text{--}45 \mu\text{m}$ in diameter, including 'spines' projecting $\pm 2.5 \mu\text{m}$ at margin, these not connected by a wing; distal face convex, with 12–16 thin, parallel, curving lamellae, $2.5 \mu\text{m}$ high (Figure 7C) running across (Figure 7A), central ones usually longer, sometimes branched, lateral ones (Figure 7D) shorter and \pm radiating, separated by $\pm 2.5 \mu\text{m}$, sometimes interconnected by slender threads (Figure 7B); proximal face (Figure 7E) mostly lacking a distinct triradiate mark, rarely more pronounced, generally orna-

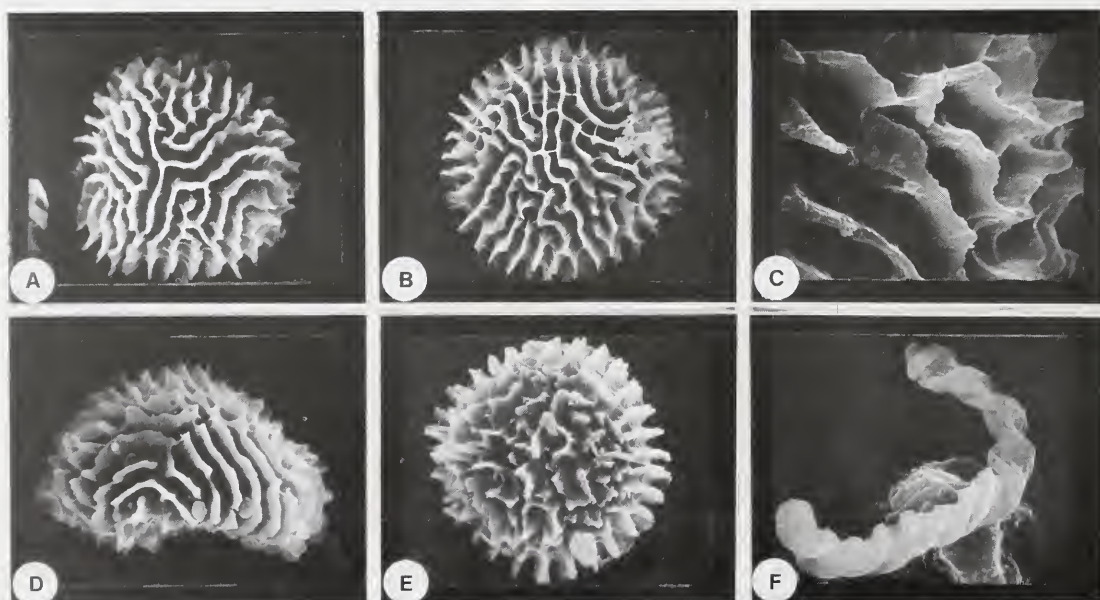


FIGURE 7.—*Fossombronía densilamellata*. Spores. A, B, distal face; C, detail of lamellae on distal face; D, side view of distal face; E, proximal face; F, elater. A, *Garside 6510*; B, *Duthie CH 1651*; C, D, *Arnell & Garside 260*; E, *S.M. Perold 629*; F, *S.M. Perold 2355*. A, $\times 719$; B, E, $\times 772$; C, $\times 2795$; D, $\times 865$; F, $\times 805$.

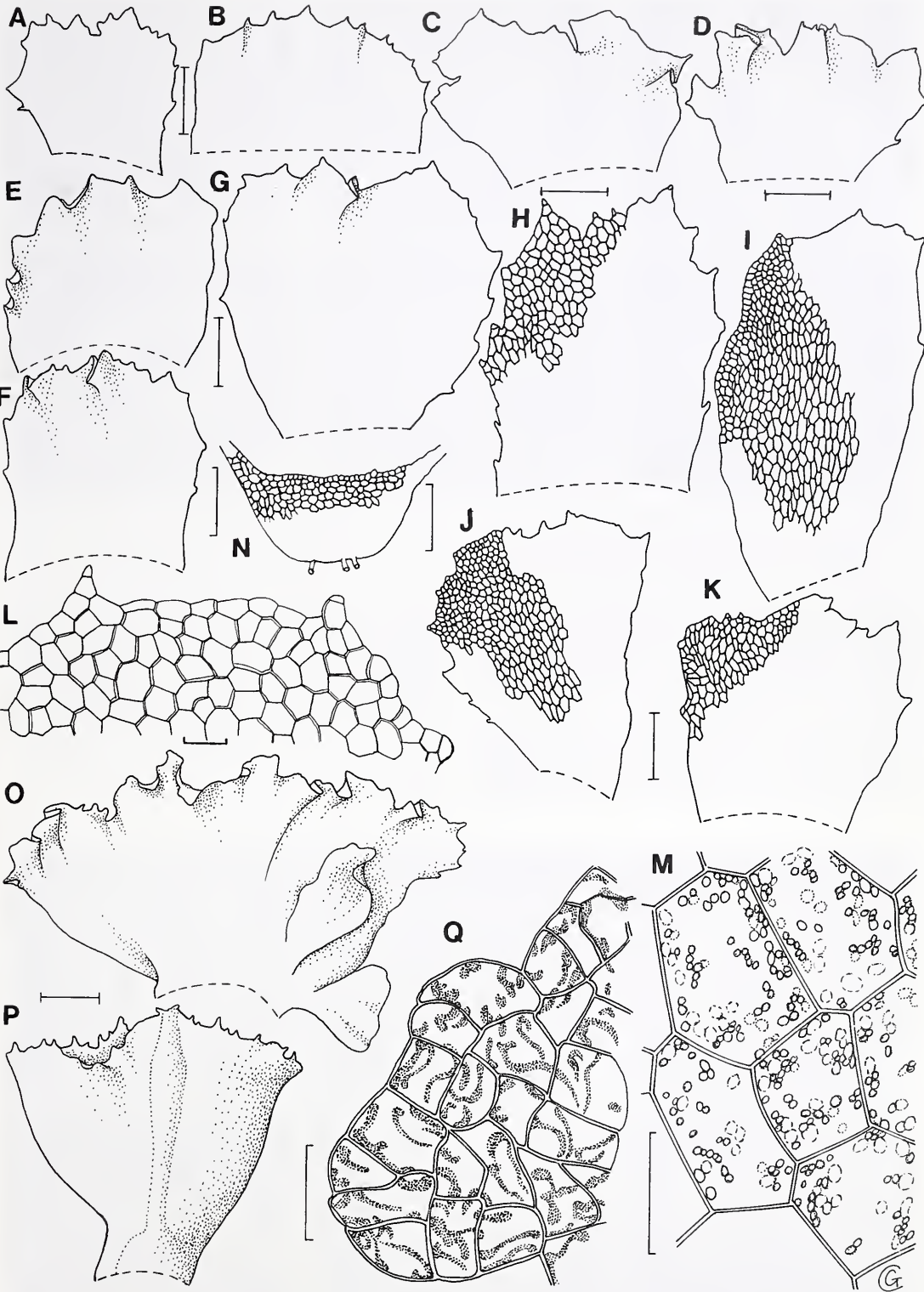


FIGURE 8.—*Fossombronina montaguensis*. A–D, young apical leaves; E, F, K, older leaves; G–J, proximal leaves; L, detail of upper margin of leaf; M, median leaf cells with oil bodies and chloroplasts mostly clumped together; N, cross section of stem; O, opened pseudoperianth; P, pseudoperianth from side; Q, cells in capsule wall. A, F–J, L–Q, S.W. Arnell 731; B, E, K, S.W. Arnell 724; C, D, S.M. Perold 3454. Scale bars: A–K, O, P, 500 µm; L, 100 µm; M, Q, 50 µm; N, 250 µm.



FIGURE 9.—*Fossombronia montaguensis*. A, thallus branches; B, apical leaves; C, female plant with archegonia; D, female plant with pseudoperianth near apex (see arrow); E, pseudoperianth from the side; F, pseudoperianth from above. A, B, *S.M. Perold 3453*; C–F, *S.W. Arnell 731*. A, $\times 12$; B, $\times 24$; C, $\times 8$; D, $\times 7$; E $\times 9$; F, $\times 11$.

mented with coarse or slender pointed processes or short, uneven ridges, around circumference up to ± 30 projecting lamellar 'spines'. *Elaters* (Figure 7F) light brown, $120\text{--}180 \times 7.5\text{--}10.0\text{ }\mu\text{m}$, tapering to tips, smooth, bispiral, rarely trispiral, occasionally branched.

Fossombronia densilamellata is known only from Western Cape and grows on partially shaded earth banks at roadsides or on river banks. It has been collected at

Kloofnek, Round House, Lion's Head, Newlands in Cape Town and at Camps Bay, as well as at Franschhoek, Stellenbosch and Algeria Forest (Figure 4). At PRE, the specimen *Arnell 762* from Cogman's Kloof, was labelled *F. densilamellata*, but the packet contains no plant material, only a slide preparation of the capsule wall without any spores; the determination could thus not be verified and Cogman's Kloof cannot with certainty be included in its distribution range.

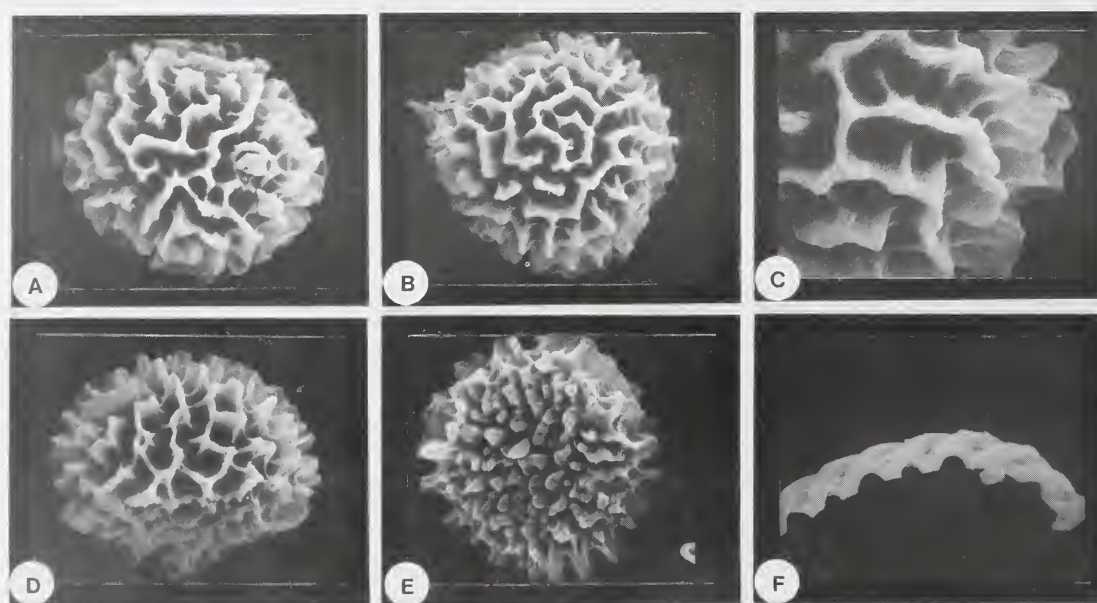


FIGURE 10.—*Fossombronia montaguensis*. Spores. A, B, distal face; C, detail of lamellae and spore surface on distal face; D, side view of distal face; E, proximal face; F, elater. A–F, *Arnell 731*. A, $\times 745$; B, $\times 699$; C, $\times 1637$; D, $\times 779$; E, $\times 759$; F, $\times 852$.

Fossombronia densilamellata is distinguished by its undulating, decurrent leaves, rare and somewhat smaller male plants with bracts shielding the antheridia and by the spore ornamentation with 12–16 narrowly spaced, thin, parallel lamellae on the distal face. The species fruits in late winter and early spring and soon dies off, and only the tuberous stem apices survive the dry summers. In specimen *S.M. Perold 2356*, from Algeria Forest, some of the capsules bore spores with thick, granular ridges, not thin lamellae; repeated samplings eventually turned up spores with typical lamellae. Arnell had previously named this species *F. confertilamellata* and his specimen 265, held at S, still bears this epithet in his handwriting. Arnell (1952) did not designate a holotype from the syntypes he cited, *Arnell 257, 265, 295, 762*. The specimen *Arnell 295* (S), is selected as lectotype because it closely matches the protologue and a duplicate is held at PRE.

Arnell (1952, 1963) seems to have overestimated the number of spines at the periphery of the spore. On SEM micrographs they appear to be nearer to 30 than to 50. Arnell (1963) refers to some similarity between the spores of *F. densilamellata* and *F. wondraczekii*. In the latter they frequently have papillae between the lamellae or sometimes the lamellae anastomose to form a few areolae in the centre. Curiously, Arnell (1952) placed '*F. tumida* Sim' in synonymy under *F. densilamellata*. He must have meant 'sensu Sim' and he seems to have misinterpreted Sim's (1926) drawing and description of the spores of *F. tumida* Mitt. The drawing correctly illustrates the significant features (although not well) and the description reads 'lamellae radiating from a few central areolae, and showing as twenty-four to thirty spines on the margin'. Arnell (1963) did not repeat these observations.

3. *Fossombronia montaguensis* S.W. Arnell in Botaniska Notiser 1952: 316 (1952); S.W. Arnell: 83 (1963). Type: Western Cape, 3320 (Montagu): Bath Kloof, (–CC), *S.W. Arnell 731* (S, lecto!, here designated).

Plants in crowded overlying mats or more loosely aggregated; leaves light green, becoming translucent or not, and then mostly darker green, later on turning yellow at margins or entirely so, sometimes juvenile leaves at apex deep red; shoots medium-sized to large, up to 10 mm long, 1.1–2.0 mm high, 1.8–3.5 mm wide, mostly repeatedly furcate, terminal segments (Figure 9A) 1–5 mm long, moderately divergent. *Stems* prostrate, green or outer layer distally purple, lateral branches occasionally developing from latero-ventral buds, plano-convex in cross section (Figure 8N), 280–380 µm high (12–14 cell rows), 490–750 µm wide, tapering toward base. *Rhizoids* purple, 10–25 µm wide. *Leaves* erect to spreading, frilly and densely crowded apically (Figure 9B), becoming spaced and lax proximally, succubous, subquadrate to long-rectangular, sometimes irregularly shaped and wider above than below, 1375–2500 × (600–) 1175–1950 µm, apical leaves (Figure 8A–D) generally smaller than more proximal ones (Figure 8E–K), frequently shorter than wide, 900–1675 × 1250–1900 µm; margins with triangular or irregular projections, with 6–16 slime papillae, ± 20 × 15 µm, often raised on a basal cell, 30–50 × 20–35 µm. *Leaf cells* at upper margins (Figure 8L) quadrate, rectangular across or irregular, 22.5–37.5 × 35.0–52.5 µm, at lateral

margins long-rectangular, 37.5–90.0 × 15.0–30.0 µm, upper laminal cells 5- or 6-sided, 32.5–45.0 × 32.5–55.0 µm, middle laminal cells 6-sided (Figure 8M), 45.0–125.0 × 25.0–62.5 µm, basal cells 50.0–155.0 × 37.5–75.0 µm. *Oil bodies* and chloroplasts were clumped together and could not be studied adequately in the available material.

?Dioicous. No male plants seen. *Archegonia* in one or two rows dorsally along stem (Figure 9C), naked, sometimes up to three per shoot becoming fertilized. *Pseudoperianth* (Figures 8O, P; 9D–F) campanulate, ± same height as leaves, sometimes slightly stalked, basally ± 875 µm wide, flaring widely above, up to 2575 µm long, 2375–3000 µm wide across cup-like mouth, its margin with ± 30 triangular protrusions on a broad base, ± 160 µm long, and topped with a papilla, 17.5 × 17.5 µm, sometimes open at side, or where two component leaves are joined, with a winged outgrowth; cells comparable in shape and size to those of leaves. *Capsules* globose or slightly flattened at the poles, 775–1050 µm in diameter, cells in inner layer of bistratose wall (Figure 8Q) irregularly shaped, 40.0–60.0 × 32.5–37.5 µm, each cell wall with 1–3 nodular and sometimes semi-annular thickenings. *Seta* 6.5–7.5 mm long, 200–275 µm in diameter. *Spores* brown, hemispherical, 40.0–47.5 µm in diameter, including lamellae projecting ± 2.5 µm at margin, not joined by a wing; distal face (Figure 10A–D) convex, with up to 10 irregularly branched, long or short, sinuous lamellae, some breaking up into spines, others interconnected by fine ridges running across, sometimes forming incomplete areolae, ± 5 × 5 µm; proximal face (Figure 10E) lacking a distinct triradiate mark, ornamented with low, irregular, rather short, branched ridges and with ± 27 irregularly shaped, variously sized, blunt, spine-like papillae projecting at circumference. *Elaters* (Figure 10F) yellow-brown, 137.5–175 µm long, ± 7.5 µm wide in centre, tips looped, ± 5 µm wide, smooth, bispiral throughout or trispiral in centre.

Fossombronia montaguensis is most frequently found on rather dryish soil banks next to footpaths in Western Cape at Bath Kloof and Cogman's Kloof, as well as at Genadendal (Figure 4), where its growth is stunted and far less luxurious than that of the lectotype specimen, *S.W. Arnell 731* (S), which must have grown in shady, damper conditions, close to water. In the specimen *S.W. Arnell 724* (S), both forms are represented: the proximal leaves are large, lax and translucent, whereas the distal leaves are smaller, firm and green, often partly stained with red. Arnell's (1952, 1963) measurements of the spores, 30–32 µm and 30–34 µm respectively, are rather less than mine. Unfortunately my own collections of *F. montaguensis* from Bath Kloof, *S.M. Perold 3453* and *3454 p.p.*, are sterile.

ACKNOWLEDGEMENTS

I wish to sincerely thank my colleagues at NBI, particularly Ms M. Koekemoer and Mrs C. Bredenkamp for their kind assistance with fieldwork; also the curators of BOL, BR, G and S as well as Dr Lübenau-Nestlé for the loan of specimens. My thanks to Ms G. Condy for the drawings, Mrs A. Romanowsky for developing and printing many photographs and Mrs J. Veldman for her part in typing the manuscript.

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- Held at PRE, unless otherwise indicated. Bracketed numbers after collectors' name and number refer to the species in the text in alphabetical order, namely: *F. capensis* (1); *F. densilamellata* (2) and *F. montaguensis* (3).
- S.W. Arnell 265 (2) S; 275, 295 (2) S (lectotype), BOL (isolectotype); 724 (3) S; 731 (3) S (lectotype); 785 (3) PRE, S; 1376 (1) S (holotype), BOL (isotype); 1470 (1) PRE, S; 1474 (1) BOL; 1477 (1) G; 1528, 1555 (1) BOL; 1678 (1) S; 1694 (1) BOL; 1715, 1716 (1) S; 1756 (1) BOL; 1757 (1) S; 1783 (1); 1851 (1) S. S.W. Arnell & Garside 215 (2) BOL, S; 259 (2) BOL; 260 (2).
- Cholnoky 388 (1) S.
- Duthie CH 1651 (2).
- Ecklon 7691 (2) W.
- Garside 6226, 6456, 6489, 6575, 6586 (2) BOL.
- Koekemoer 998 (1).
- Lübenau-Nestlé SA 139/2 (1) pte.herb.
- S.M. Perold 629 (2); 919 (1); 2355, 2356 (2); 3343, 3346, 3347, 3349 (2); 3453, 3454 pp. (3); 3492, 3494, 3497, 3498 (1); 3534, 3539, 3540–3541 (1).
- S. Russell 2530 (1).
- Van Zanten et al. 7609809 pp. (2).

Studies in the liverwort genus *Fossombronina* (Metzgeriales) from southern Africa. 3. An amendment to *F. spinifolia*

S.M. PEROLD*

Keywords: *Fossombronina*, *F. spinifolia*, Hepaticae, Metzgeriales, southern Africa

ABSTRACT

Fossombronina spinifolia was described by Stephani (1900) from a specimen collected by Breutel at Genadendal (Gnadenthal) during his visit to the Cape, which lasted from November 1853 to April 1854 (Gunn & Codd 1981). This species was not adequately described and illustrated by Stephani or by subsequent workers. Moreover, Scott & Pike (1987) misapplied the epithet, *F. spinifolia*, to specimens Arnell had identified as *F. leucoxantha*, because they (Scott & Pike 1988) overlooked a capsule with ripe spores in the type specimen. An attempt is hereby made to describe and illustrate this species in greater detail in order to prevent more confusion in future.

Fossombronina spinifolia Steph. in Species hepaticarum 1: 389 (1900); Sim: 36 (1926); S.W.Arnell: 84 (1963). Type: Africa Australis, Gnadenthal, leg. Breutel s.n. G 22186, ex herb. K. Müller Halensis (holo!).

Plants in dense, overlying mats, green to dark green, leaf margins occasionally yellowed or those of proximal ones tinged with red to purple, rather small and slender; shoots mostly simple, 3.0–7.0 mm long, 1.0–1.2 mm high, 1.7–2.5 mm wide, generally arising from fleshy, tuberous apices (Figure 2A) and laterally from sides of older, mostly leafless stems of various length (Figure 2B), that taper proximally to thin, narrow bases. Stems bearing leaves prostrate, these in turn tapering distally, mostly plano-convex in cross section, in male plants at apex (Figure 1M) ± 170 μm (10 cell rows) high, ± 210 μm wide, at base (Figure 1N) 230–240 μm (10 cell rows) high, ± 250 μm wide; in female plants at apex (Figure 1O) 230–240 μm (12 cell rows) high, up to 380 μm wide, at base (Figure 1P) ± 360 μm (14 cell rows) high, ± 500 μm wide. Rhizoids purple, 12.5–22.5 μm wide, absent from shoot apices. Leaves in male plants (Figure 1A–E) closely spaced, but rarely overlapping, spreading, succubously inserted on stem, oblong to irregularly shaped, 700–1175 \times 500–1500 μm , sometimes narrower below, upper margin mostly markedly dentate, with up to 10 teeth, these occasionally expanded into 1 or 2 triangular lobes; in female plants, leaves (Figure 1F–J) spreading to suberect, overlapping (Figure 2E), frequently ‘ruched’ above, very obliquely succubously inserted, leaving stem exposed, shape irregular, as long as wide, 875–1000 \times 800–1075 μm , but sometimes shorter than wide, 1050–1200 \times 1300–1625 μm , upper margin (Figure 1K) dentate but often less pronouncedly so than in male leaves, more often with triangular lobes. Leaf cells not appreciably different in male and female plants, thin-walled, at margins subquadrate to rectangular across, 20.0–35.0 \times 32.5–57.5 μm , in male plants teeth 112.5–270.0 μm long, composed of an apical slime papilla, $\pm 12.5 \times 12.5$ μm , followed below by 1–3 single, long-rectangular cells arranged end to end, 27.5–50.0 \times 17.5–40.0 μm , gradually broadening to base, usually with 2 or 3 (oc-

asionally more) cells alongside each other, margins in female plants with up to 12 well-spaced papillae, at lower lateral margins cells long-rectangular, 42.5–50.0 \times 17.5–25.0 μm , upper laminal cells 5- or 6-sided, 30.0–37.5 \times 32.5–40.0 μm , middle laminal cells 47.5–52.5 \times 32.5–37.5 μm , basal cells 50.0–62.5 \times 40.0–50.0 μm . Oil bodies absent from most cells; chloroplasts clumped together along cell walls, ± 5 μm in diameter (Figure 1L).

Dioicous. Antheridia dorsal on stem (Figure 2C, D), in a row, short-stalked, globose, ± 280 μm in diameter, each shielded by a perigonial bract (Figure 1Q–T), 300–450 \times 200–400 μm , margins with 1 or 2 (3) teeth and 2–5 papillae, cells in interior 5- or 6-sided, 52.5–75.0 \times 27.5–37.5 μm . Archegonia in a well-spaced row along stem (Figure 2F), ± 280 μm long. Pseudoperianth (Figure 1U, V) turbinate, near stem apex, mostly projecting somewhat above leaves, from narrow base flaring widely above, ± 1625 μm long, 1500 μm wide across mouth, margin with several very long teeth, 7–12 cells or up to 385 μm long, consisting of an apical papilla followed below by 4 single, long-rectangular cells, arranged end-to-end and then basally by 3–5 cells in pairs, the rest of the cells comparable in shape and size to those of leaves. Capsule globose, diameter could not be measured as it was no longer intact, wall bistratose, cells in inner layer (Figure 1W) irregularly shaped, 35.0–42.5 \times 20.0–30.0 μm , each cell wall with 1 or 2 yellow or brown nodular and sometimes semi-annular thickenings. Seta 1.4–3.5 mm long, ± 100 μm in diameter. Spores yellow-brown, hemispherical, 36.0–45.0 μm in diameter, including spines projecting around periphery; distal face convex, with 6 or 7 short irregular ridges ± 5 μm apart and sometimes branched (Figure 3B, C), sides of ridges and surface between them with fine cross striations and granules (Figure 3D), papillae occasionally interspersed in between (Figure 3A); proximal face (Figure 3E) lacking triradiate mark, flat to slightly concave, covered with numerous irregular papillae, around spore periphery up to 25 projecting, ‘spines’, some conical, others truncate. Elaters (Figure 3F) light brown, 105.0–150.0 \times 7.5 μm , tapering to looped tips, 3–5 μm wide, some completely bispiral, others partly bi- and trispiral.

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MS. received: 1997-01-10.



FIGURE 1.—*Fossombronina spinifolia*. A–E, male leaves; F–J, female leaves; K, detail of leaf margin of female leaf; L, median leaf cells with remains of oil bodies (solid lines) and chloroplasts (dotted lines); M, cross section of male stem apex; N, cross section of male stem base; O, cross section of female stem apex; P, cross section of female stem base; Q–T, bracts; U, opened pseudoperianth; V, pseudoperianth from side; W, cells in capsule wall. A, F–I, U–W, *Breutel s.n. G 22186*; B–E, J–T, *Breutel s.n. (W)*. Scale bars: A–J, U, V, 500 μ m; M–T, 250 μ m; K, L, W, 50 μ m.

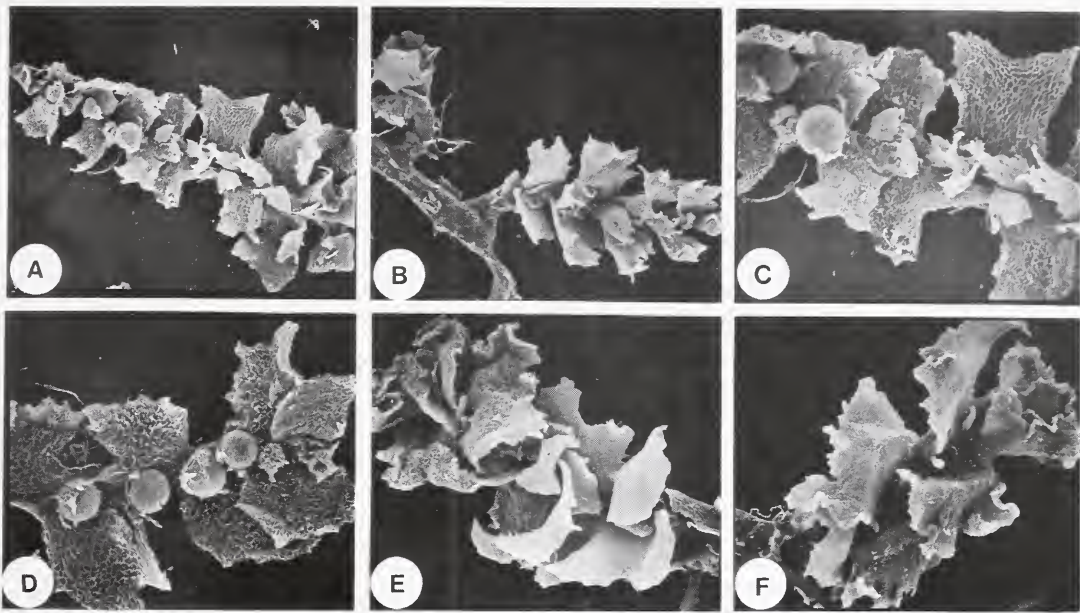


FIGURE 2.—*Fossombronía spinifolia*. A, male branch which arose from apex of older stem; B, two branches arising from side of older, mostly leafless stem; C, D, close view of antheridia and bracts; E, F, larger female branches with suberect, overlapping leaves and archegonia along stem. A–F, *Breutel s.n.* (W). A, $\times 13.5$; B, $\times 15.4$; C, D, $\times 24.3$; E, $\times 18.2$; F, $\times 14.5$.

Fossombronía spinifolia is known only from Genadendal, in Western Cape (Figure 4), where it was collected by Breutel, probably in November or early December 1853, at the start of his visit to the Cape, which included various halts along the way, ending at Hankey in the Eastern Cape (Gunn & Codd 1981). The holotype specimen, *Breutel s.n.* G 22186, consists of a few fragments, which were originally housed in Müller’s herbarium and upon his death in 1899, were acquired by Stephani. The packet

in G contains Stephani’s well-preserved preparations of several leaves, leaved branches and pseudoperianths, which I measured and photographed. The *Icones No. 003053* (Stephani 1985) illustrate, however, only a single dentate leaf, a spore with numerous spines around the circumference and an elater. One of the fragments of the type specimen contains a single antheridium, 2 fragments have immature capsules and another consists of a branch with a pseudoperianth containing a broken capsule with

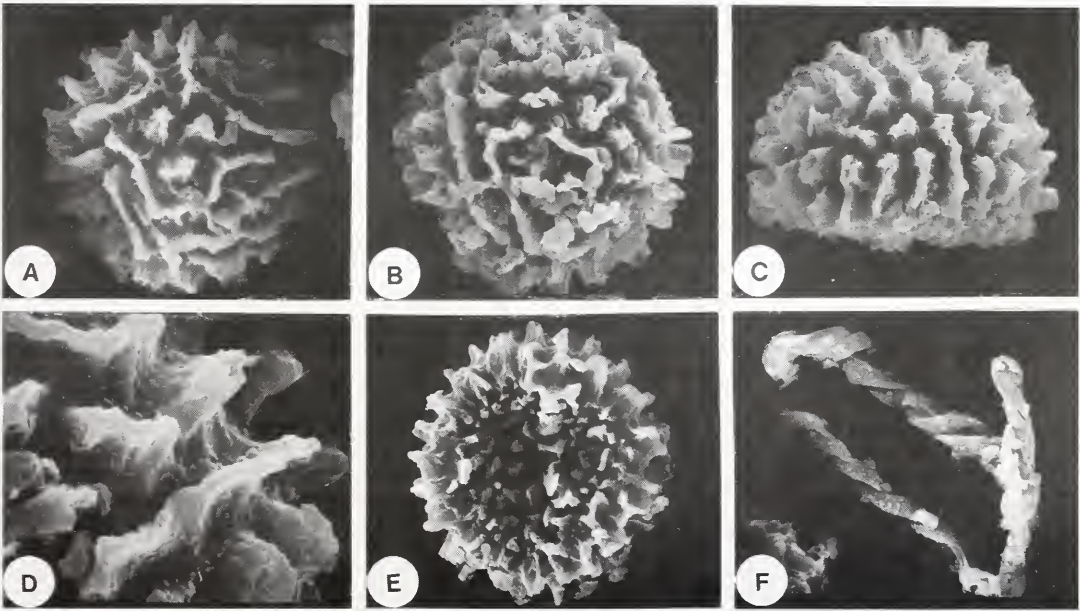


FIGURE 3.—*Fossombronía spinifolia*. Spores. A, B, distal face; C, side view of distal face; D, detail of lamellae at margin of distal face; E, proximal face; F, elaters. A–F, *Breutel s.n.* G 22186. A, $\times 870$; B, $\times 987$; C, $\times 940$; D, $\times 2434$; E, $\times 856$; F, $\times 866$.

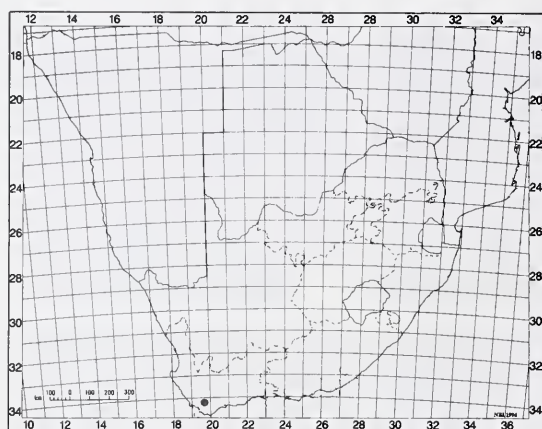


FIGURE 4.—Distribution of *F. spinifolia* in southern Africa.

mature spores. The spores were overlooked by Scott & Pike (1988) and they (Scott & Pike 1987) had previously misapplied the epithet *F. spinifolia* to specimens Arnell had identified as *F. leucoxantha* (Perold 1997 in press). Sim (1926) reports *F. spinifolia* from Jonker's Hoek, Stellenbosch, Genadendal and other southwestern localities. The Jonker's Hoek specimen has not been seen, but the two Stellenbosch specimens, *H.A. Wager 34* (CH1650) and *Duthie 3* (CH1651), are held at PRE. They have, however, been misidentified. Another *Breutel s.n.* specimen from Genadendal is on loan to PRE from W. It had been determined as *F. pusilla*, but there is no doubt that it is *F. spinifolia*, although unfortunately it lacks pseudoperianths and spores. The specimen is mixed with a fragment of another *Fossombronina* species; it has pseudoperianths with a few low spines at the margin and spores unlike those of *F. spinifolia*. The material of *F. spinifolia* from W comprises numerous specimens, but the leaf cells are rather less well preserved than those in Stephani's preparations. There are several male plants with mature antheridia and a few female plants with archegonia only. Preparations from this specimen were also measured and photographed by LM as well as SEM.

In an attempt to collect fresh material of *F. spinifolia*, I paid a brief visit to Genadendal in October 1995, but failed to find any. The streambanks, which are the most likely site where the species would be found (the exact locality was not stated on the label), are much disturbed and there has also been considerable infestation by alien plants.

SPECIMENS EXAMINED

Breutel s.n. G22186 (holo.!) ex herb. K. Müller Halensis; *W s.n.*

ACKNOWLEDGEMENTS

I wish to sincerely thank Mrs Diana Harvey, honorary horticulturalist at Genadendal, for her hospitality and assistance with fieldwork; also Mrs C. Bredenkamp, assistant curator, National Botanical Institute, for all her help and support. The curators of G and W are warmly thanked for the loan of specimens and I extend my sincere thanks to Ms G. Condy for the drawings, Mrs A. Romanowski for developing and printing the photographs and to Ms D. Maree for typing the manuscript.

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Notes on African plants

VARIOUS AUTHORS

FABACEAE

A SURVEY OF ANTIPODALS IN THE GAMETOPHYTE OF THE TRIBES PODALYRIEAE AND LIPARIEAE

Antipodal cells in the female gametophyte of the Fabaceae are variable (Prakash 1987). In the Mimosoideae and Caesalpinioidae, antipodals tend to persist at least until fertilization, whereas they are mostly ephemeral in the Papilionoideae (George *et al.* 1979; Prakash 1987). The variation found in papilionoid antipodals up to 1990, is summarized by Cameron & Prakash (1990, 1994).

In a detailed study of antipodal behaviour in the Australian Bossiaceae and Mirbelieae, Cameron & Prakash (1990, 1994) established that antipodals are of considerable taxonomic value at the tribal level. They found giant antipodals in the gametophytes of some genera of the tribes, and ephemeral or no antipodals in the remaining genera. These results evidently supported tribal rearrangements proposed earlier by Crisp & Weston (1987).

Relationships amongst the genera of the tribes Podalyrieae and Liparieae have recently been investigated (Schutte 1995; Van Wyk & Schutte 1995; Schutte & Van Wyk 1997a). The study showed that the two tribes are monophyletic, but that the genus *Hypocalyptus* is incongruous. In view of these results and suggestions by Crisp & Weston (1987), that the Australian tribes may be closely related to the Podalyrieae and Liparieae, it was decided to examine the antipodals of the two tribes as an additional character. The results are presented and discussed here.

MATERIALS AND METHODS

At least one species of each genus of the Podalyrieae and Liparieae *sensu* Polhill (1976, 1981a, b) was included in the study. Voucher specimens of the material examined are listed in Table 1.

Buds (just prior to anthesis) were fixed in an ethyl alcohol-water-glycerol (70:29:1, v/v) mixture. Ovules were dissected from the buds and serially dehydrated and embedded in glycol methacrylate (GMA) according to the method of Feder & O'Brien (1968). These were sectioned with an ultramicrotome, stained in Toluidine Blue and mounted in Eukitt.

RESULTS AND DISCUSSION

From the results summarized in Table 1, it is clear that antipodal cells are present in both tribes. The antipodals are prominent and persistent at least until anthesis in *Liparia*, *Xiphotheca*, *Amphithalea*, *Coelidium* and the genera of the Podalyrieae (Figure 1). *Cyclopia* in particular, has large and deeply stained nuclei in the cells (Figure 1C). *Hypocalyptus*, however, has inconspicuous and ephemeral antipodal cells (Figure 1F), which degenerate before anthesis (several ovules had to be sectioned before the antipodals could be traced).

Unlike the Bossiaceae and Mirbelieae, antipodals are neither gigantic nor totally absent in the Podalyrieae and Liparieae. In the latter two tribes they are less than 0.25 times the length of the gametophyte cavity (Figure 1), compared with the Australian genera, where they are more than 0.5 times the length of the gametophyte cavity (see figures in Cameron & Prakash 1990, 1994). These giant antipodals persist until well after fertilization. A direct link between the Australian and South African tribes therefore seems unlikely.

The presence of persistent antipodals in the female gametophyte of the Podalyrieae and Liparieae (excluding *Hypo-*

TABLE 1.—List of species examined and the characteristics of the antipodal cells. Voucher specimens are housed in JRAU

Taxon	Voucher	Antipodals
PODALYRIEAE		
<i>Cyclopia sessiliflora</i> Eckl. & Zeyh.	Vlok 2627	Persistent
<i>Podalyria burchellii</i> DC.	Vlok & Schutte 78	Persistent
<i>Stirtonanthus taylorianus</i> (L.Bolus) B-E.van Wyk & A.L.Schutte	Van Wyk 3248	Persistent
<i>Virgilia oroboides</i> (P.J.Bergius) T.M.Salter subsp. <i>oroboides</i>	Schutte 534	Persistent
LIPARIEAE		
<i>Amphithalea tomentosa</i> (Thunb.) Granby	Vlok & Schutte 64	Persistent
<i>Amphithalea violacea</i> (E.Mey.) Benth.	Vlok & Schutte 9	Persistent
<i>Coelidium vlokii</i> A.L.Schutte & B-E.van Wyk	Schutte 665	Persistent
<i>Hypocalyptus coluteoides</i> (Lam.) Dahlgren	Schutte 730	Ephemeral
<i>Hypocalyptus sophoroides</i> (Berg.) Baill.	Schutte 480	Ephemeral
<i>Liparia genistoides</i> (Lam.) A.L.Schutte	Schutte 752	Persistent
<i>Xiphotheca canescens</i> (Thunb.) A.L.Schutte & B-E. van Wyk	Vlok & Schutte 46	Persistent
<i>Xiphotheca phycioides</i> A.L.Schutte & B-E.van Wyk	Vlok 2640	Persistent

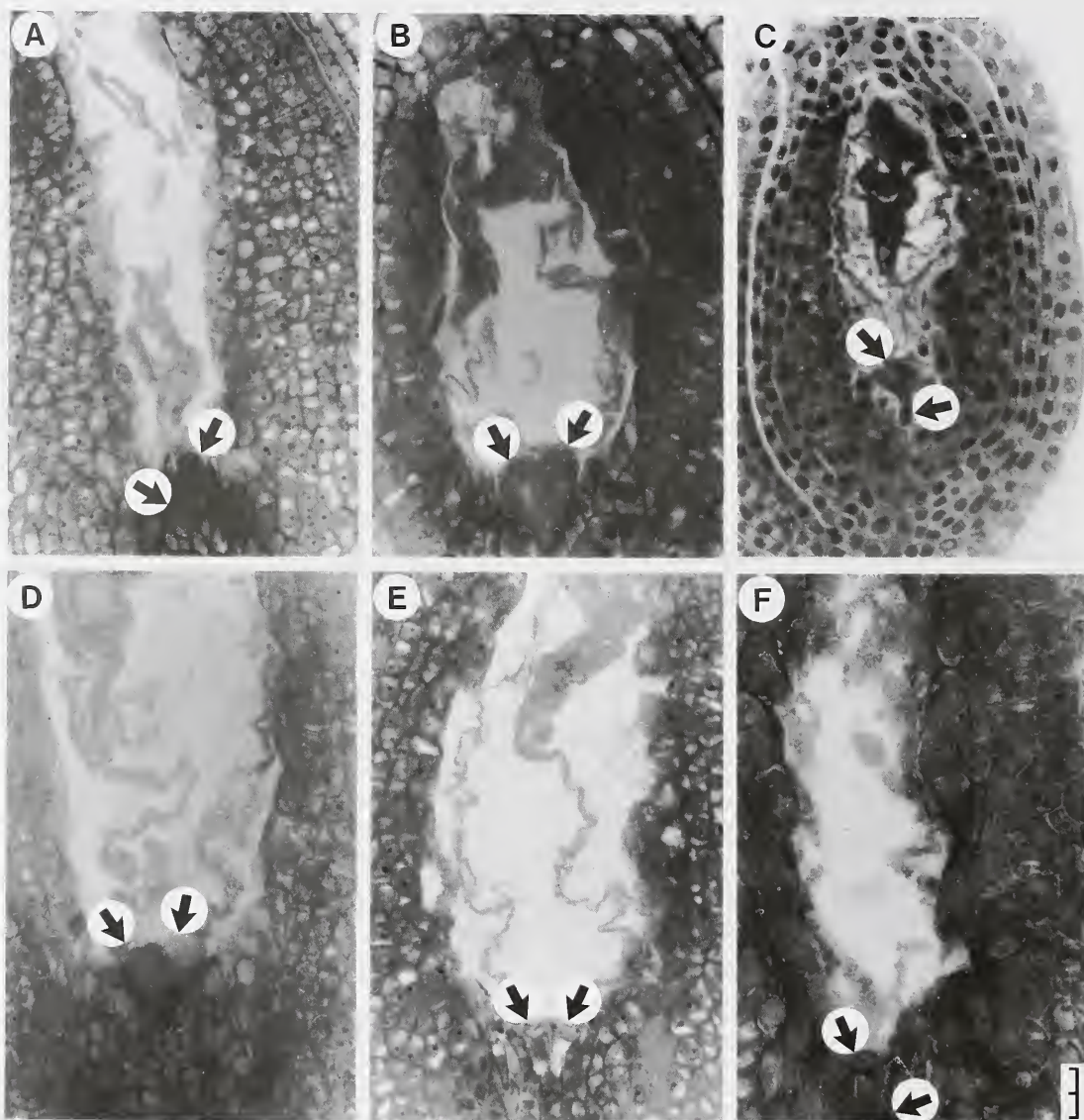


FIGURE 1.—Female gametophytes of some species of Podalyrieae and Liparieae, showing the antipodals (indicated with arrows). A, *Stirtonanthus taylorianus*; B, *Virgilia oroboides* subsp. *oroboides*; C, *Cyclopia sessiliflora*; D, *Amphithalea tomentosa*; E, *Coelidium vlokii*; F, *Hypocalyptus sophoroides*. Scale bar: 50 μ m.

calyptus) is a synapomorphy for the two tribes. In the tribe Crotalariae, which is the sister group of the Podalyrieae and Liparieae (Schutte & Van Wyk 1997a), antipodals are ephemeral (Narang 1978; Schutte unpubl.). The proposed amalgamation of the two tribes is therefore clearly supported by the antipodal characteristics. Other characters, such as the strongly reduced bracteoles and the accumulation of esters of anthocyanins in the pink, purple or orange-flowered species, also support this notion (Schutte & Van Wyk 1997a).

Hypocalyptus not only deviates from the other genera in its antipodal characteristics, but also in at least eight other significant morphological, cytological and chemical characters (Schutte & Van Wyk 1997b). This undoubtedly indicates that the genus does not fit in the Podalyrieae *sensu lato*. The tribal position of *Hypocalyptus* within the

Papilionoideae will be re-assessed and discussed elsewhere (Schutte & Van Wyk 1997b).

ACKNOWLEDGEMENTS

I am very grateful to Dr P.M. Tilney (Department of Botany, RAU) for assisting with the preparation of the microscope slides and to Prof. B.-E. van Wyk (Department of Botany, RAU) for commenting on an earlier draft of the manuscript. Financial support from the Rand Afrikaans University is acknowledged.

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THYMELAEACEAE

NEW COMBINATIONS IN *LACHNAEA*

The genus *Cryptadenia* Meisn. comprising five species, was established by Meisner in 1840 and based on Drège's collections (Meisner 1840). In De Candolle's *Prodromus* the same five species were recognized by Meisner (1857). Wright (1915) in his treatment of the genus recognized four of these species, reduced one to synonymy and described a new species. Beyers & Van der Walt (1995) concluded that *Cryptadenia* and *Lachnaea* L. are congeneric and that *Cryptadenia* should be included within *Lachnaea*. In accepting these findings, the necessary nomenclatural changes are made to the five species which are currently recognized (Van Wyk 1993) following Wright's treatment of the genus.

Lachnaea filicaulis (Meisn.) Beyers comb. nov.

Cryptadenia filicaulis Meisn.: 407 (1840); Meisn.: 574 (1857); C.H.Wright: 17 (1915).

Lachnaea grandiflora (L.f.) Baill.: 109, t. 77 (1880).

Passerina grandiflora L.f.: 226 (1782). *Cryptadenia grandiflora* (L.f.) Meisn.: 405 (1840); Meisn.: 573 (1857); C.H.Wright: 16 (1915).

Cryptadenia breviflora Meisn.: 406 (1840); Meisn.: 573 (1857); C.H.Wright: 17 (1915). Type: *Ecklon* 360 (?holo, K!; NBG!, iso.).

Lachnaea laxa (C.H.Wright) Beyers comb. nov.

Cryptadenia laxa C.H.Wright: 17 (1915).

Lachnaea uniflora (L.) Beyers comb. nov.

Passerina uniflora L.: 560 (1753). *Cryptadenia uniflora* (L.) Meisn.: 406 (1840); Meisn.: 573 (1857); C.H.Wright: 16 (1915).

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RUBIACEAE

A NEW SPECIES OF *VANGUERIA* FROM THE SOUTPANSBERG

Vangueria soutpansbergensis N. Hahn sp. nov. *V. parvifolia* Sond. [= *Tapiphyllum parvifolium* (Sond.) Robyns ex Good] affinis sed foliis glabris. Figure 2.

TYPE.—Northern Province, Soutpansberg, 2230 (Messina), Farm Studholme, 22° 56' 52.4" South and 30° 01' 18.8" East (Cape Mapping Datum), (–CC), 1 440

m, 28-11-1995, (in flower), *N. Hahn 1112* (PRU, holo.; K, PRE, iso.).

A deciduous shrub or small tree up to 2.5 m high, growing in mixed woodlands in soils derived from Soutpansberg Group quartzites. *Bark* dark brown to grey-brown. *Branches* glabrous. *Leaves* opposite or fascicled, if fascicled usually on dwarf lateral branches; lamina elliptic to almost circular, (13.6–)16.2–25.2(–26.7) × (9–)12.9–18.9(–22.8) mm; base obtuse to rounded; apex obtuse to rounded; glabrous above and below, seldom very sparsely hairy when young, dark green above, paler below; petiole short, (0.5–)1.1–2.4(–2.7) mm long, glabrous to rarely sparsely hairy; margins entire; lateral veins 3–5, opposite to alternate near the leaf base, otherwise alternate. *Inflorescence*: dense 2–15-flowered fascicles or peduncu-

late cymes. *Peduncle* and *pedicel* glabrous or very sparsely hairy, pedicel (1.5–)2.1–2.9(–3.7) mm long. *Flowers* 5-merous, greenish to lime-green. *Calyx lobes* (1.2–)1.7–1.9(–2.6) × (1–)1.3–1.4(–1.9) mm, glabrous to sparsely hairy. *Corolla* glabrous to sparsely hairy on outside, with a distinct ring of reflexed hairs in throat; tube (2.3–)2.5–2.7(–3.2) mm long, (2.1–) 2.5–2.8(–3.4) mm in diameter at mouth; lobes elliptic-oblong (2.9–)3.3–3.5(–4.1) mm long, occasionally mucronate abaxially at apex. *Stamens* inserted in corolla mouth. *Anthers* exserted, (0.9–)1.3–1.4(–1.6) mm long. *Style* (3.1–)3.6–3.9(–4.6) mm long, glabrous, conversely curved so as to touch throat of tube between two anthers. *Disc* (1.8–)2.2–2.3(–2.8) mm in diameter, depressed or tumid. *Hypanthium* (1.1–)1.6–1.7(–2.1) mm long. *Fruit* a glabrous, subglobose drupe, length (15.3–)17.9–24.1

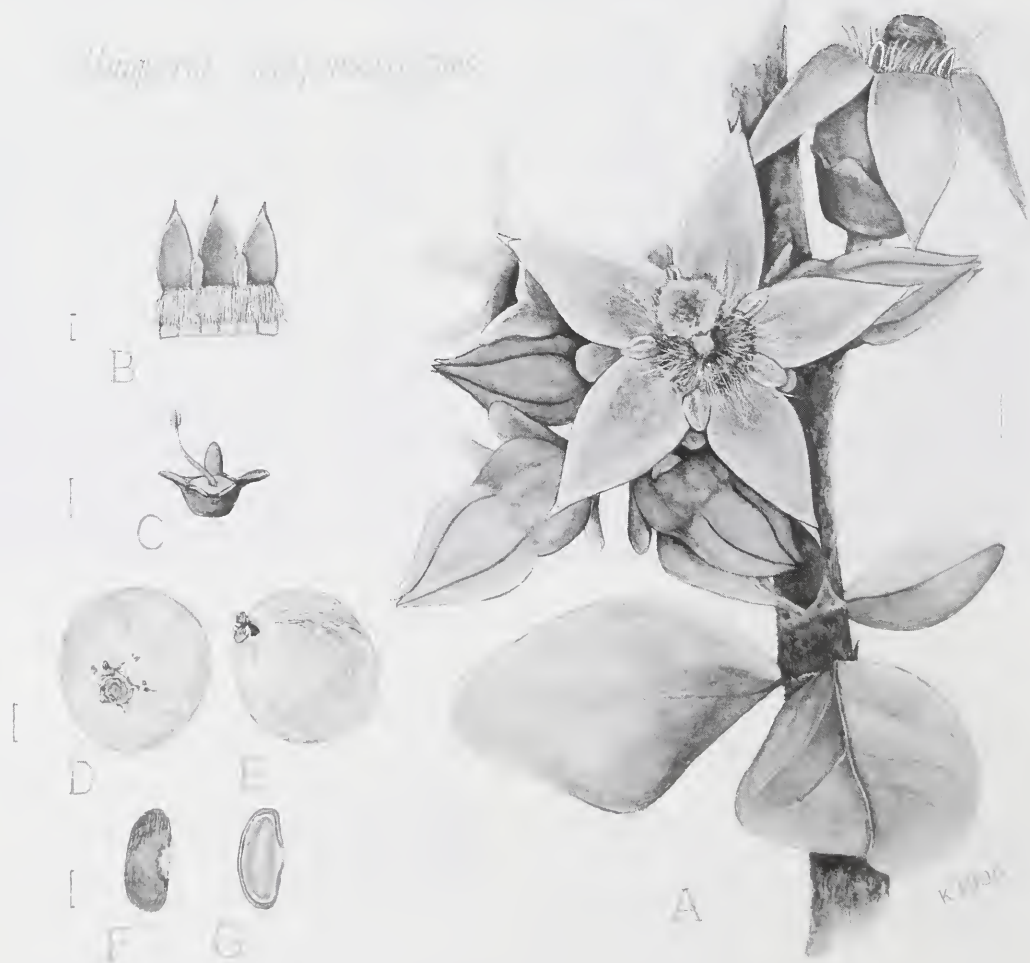


FIGURE 2.—*Vangueria soutpansbergensis*. A, flowering branch; B, opened corolla, showing hair fringes and position of anthers; C, flower with tube removed, showing calyx, disc and conversely curved style; D, fruit seen from the base, showing the remains of the calyx ring; E, side view of fruit; F, pyrene; G, cross section through pyrene, showing shape and position of embryo. Scale bars: A, B, ± 1 mm; C, ± 2 mm; D–G, ± 10 mm.

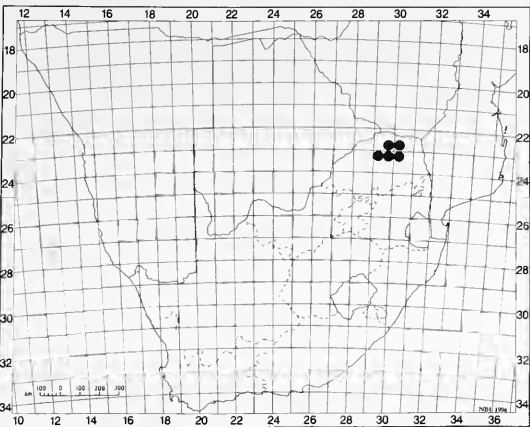


FIGURE 3.—The known distribution of *Vangueria soutpansbergensis*.

(–27.5) mm, width (14.7–)17.5–25.9(–29.4) mm, breadth (13.6–)16.3–23.7(–27.2) mm; pedicel (0.5–)0.8–1.9 (–2.3) mm long, with 1–4 pyrenes, edible, tasting similar to those of *V. infausta*; seeds bean-shaped. Flowering period: November to December. Fruiting period: March to April.

Specimens examined

NORTHERN PROVINCE.—2229 (Waterpoort): Muswiru, Schlesingers sawmill, (–DC), *G. Gerstner* 5912 (K n.v., PRE); Farm Surprise, (–DC), *N. Hahn* 454 (Herb. Sout.); Farm Uniondale, (–DC), *N. Hahn* 329 (PRU, Herb. Sout.); Farm Clydesdale, (–DD), *N. Hahn* 613 (Herb. Sout.); Farm Rushton, (–DD), *N. Hahn* 650 (Herb. Sout.); Farm Zwarthoek, (–DD), *N. Hahn* 109 (PRU, Herb. Sout.). 2230 (Messina): Piesanghoek, (–AA), *G. Gerstner* 5736 (PRE); Farm Studholme, (–AA), *N. Hahn* 1112 (K, PRE, PRU, Herb. Sout.); *N. Hahn* 1164 (K, PRU, Herb. Sout.).

Habitat

The geographic distribution of this species correlates with other endemic taxa of the Soutpansberg flora. A phytogeographical survey of the endemic flora of the Soutpansberg (Figure 3) being undertaken by the author has shown that the endemic species of the Soutpansberg can be divided into two broad groups according to their habitat preferences, namely: 1, species occurring in a relatively restricted area and displaying little variation in their habitat preference; 2, species distributed over most of the mountain range showing a relatively large habitat tolerance. *Vangueria soutpansbergensis* falls within the latter group, occurring in a variety of habitats ranging from mountain mistbelt to *Androstachys* woodland.

Generic disposition

Having studied all members of the genera *Pachystigma*, *Vangueria*, *Lagynias* and *Tapiphyllum* in the context of the Soutpansberg, I conclude that the flowering structures and fruiting structures of *Tapiphyllum parvifolium* are identical to those of *Vangueria*. Bridson (1996) expressed doubt as to the generic dispensation of *Tapiphyllum parvifolium* as it was atypical of the genus in many respects: ‘small leaves, few-flowered inflorescence, larger glabrescent fruit and occurring outside the main distribution area of the rest of *Tapiphyllum*’. *Tapiphyllum*

parvifolium and *V. soutpansbergensis* are without doubt closely related. This supports the argument that they should be placed under the genus *Vangueria*.

Key to genera of the tribe Vanguerieae in the Soutpansberg region

- 1a Calyx lobes short, linear or triangular, shorter than the corolla tube *Vangueria*
- 1b Calyx lobes long and leafy, as long as or longer than the corolla tube:
 - 2a Calyx lobes spatulate; fruit narrowing towards apex . . . *Lagynias*
 - 2b Calyx lobes linear; fruit not narrowing towards apex . . . *Pachystigma*

Specific disposition

The tribe Vanguerieae is notorious for its taxonomic complexities. The genera are poorly defined, and at specific level, characters available for the separation of taxa are very few and at best can be seen as very artificial. The morphological differences between *Vangueria soutpansbergensis* and *V. parvifolia* are very slight and concern mainly the degree of hairiness of various organs (Table 2). *V. soutpansbergensis* is nevertheless recognized at species level for the following reasons: a) other similarly closely related species pairs are widely recognized in Rubiaceae, for example, *Vangueria infausta* subsp. *infausta* and *V. cyanescens* and *Canthium mundianum* and *Canthium gilfillanii*; b) even though *V. soutpansbergensis* and *V. parvifolia* are sympatric in some places no intermediate forms have been found; c) *V. soutpansbergensis* is endemic to the Soutpansberg, a region with a high occurrence of endemic plants and animals.

Vangueria soutpansbergensis is by no means a rare plant, usually occurring within mixed woodlands, on rocky slopes where it may be common. The species has so far only been found growing on soils derived from quartzite, an attribute shared with most endemic plant species of this region.

ACKNOWLEDGEMENTS

I hereby would like to thank the National Botanical Institute Pretoria for allowing me access to their library and herbarium. I am grateful to Prof. Braam van Wyk (Curator, Schweickardt Herbarium, University of Pretoria) for his

TABLE 2.—Summary of characters separating the two species of *Vangueria*

	<i>V. soutpansbergensis</i>	<i>V. parvifolium</i>
Distribution	restricted to Soutpansberg	occurring from Northern Cape to Northern Province and within southeastern Botswana
Bark colour	grey to dark brown	grey to grey-brown
Young branches	glabrous, seldom sparsely hairy	tomentose
Outside corolla	glabrous to sparsely hairy	densely hairy
Calyx	glabrous to sparsely hairy	densely hairy
Pedicel	glabrous	hairy

assistance and for allowing me access to that herbarium. I would also like to thank Ms Diane Bridson for scrutinizing the original manuscript and for her invaluable comments given. Lastly I would like to thank Karen Marais for her beautiful water colour plate accompanying this article.

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- MS. received: 1996-10-17.

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ASTERACEAE

NEW COMBINATION IN *DICOMA*

In the course of extensive studies of herbarium material of various genera of the tribes Mutisieae and Inuleae (Asteraceae) from sub-Saharan Africa, we have noted new localities and other data for species of *Dicoma* Cass. (Mutisieae).

Dicoma membranacea S.Moore

Although *D. membranacea* S.Moore has been considered by various authors (Moore 1904; Wilson 1923; Merxmüller 1967) to be closely related to *D. sessiliflora* Harv., nobody to date has questioned the species status of this taxon; this may be because the currently accepted distribution of *D. membranacea* (northwest Namibia and southern Angola) (Figure 4) does not overlap either with that of *D. sessiliflora* subsp. *sessiliflora*—Malawi, Tanzania, Mozambique and parts of Zaïre (Pope 1992)—or with that of the recently described *D. sessiliflora* subsp. *stenophylla* Pope in West Africa (Pope 1991). However, we have examined the material from Mozambique cited below, and currently referred to subsp. *sessiliflora*, which is morphologically indistinguishable from *D. membranacea* from Angola and Namibia.

We found *D. sessiliflora* and *D. membranacea* to differ only in length of stem (less than 150 mm tall in the latter). Moore (1904) considered the presence of pedunculate capitula to be diagnostic for *D. membranacea*, but we have examined specimens of this taxon in which the capitula are sessile [Voucher: Angola, *Rui Correia* 2589 (LUAI)] or subsessile [Vouchers: Angola, *Borges* 123 (LUAI); Mozambique, *Gomes e Sousa* 2157 (COI)], and furthermore the capitula of *D. sessiliflora* are not always sessile. Moore (1904) considered corolla size to discriminate between the two taxa, but the size cited by this author for *D. membranacea* is the same as that given by Pope (1992) for *D. sessiliflora*. Similarly, Moore (1904) stated that the corolla lobes are the same length as the tube in *D. membranacea*; this is not the case in a number of specimens examined by us in which the lobes are longer than the tube [including those of *Rui Correia* 2589, *Borges* 123 and *Giess* 8969 (K) from Namibia]. In our opinion the putatively distinguishing characters included in Pope's (1991) key to the section *Pterocomma* are, with the exception of length of stem (maximum 150 mm in *D. membranacea*), likewise of limited value. This author cites stem hairiness as a distinguishing character and states that

only the stems of *D. sessiliflora* can be glabrescent. We have not been able to identify clear differences between the two taxa in this respect, and have found specimens of *D. membranacea* with glabrescent stems [Voucher: Angola, *Borges* 123 (LUAI)]. We did not find significant differences with regard to length of leaves (more than 120 mm long in *D. sessiliflora* versus up to 100 mm long in *D. membranacea*); indeed Moore (1904) described *D. membranacea* as having leaves up to 140 mm long.

MOZAMBIQUE.—1235: Inhambane, Massinga-Vilanculos, Govuru River, 7-1938, *Gomes e Sousa* 2157 (COI, K, LISC). 2335: Niassa, Administrative Post of Mujoco, 30-9-1948, *Pedro & Pedrogão* 5449 (LMA).



FIGURE 4.—Distribution of *Dicoma sessiliflora* subsp. *sessiliflora* var. *membranacea*. Known distribution based on Moore (1904), Merxmüller (1967) and herbarium material: dotted area. New localities: triangles.

Since the morphological differences between these two taxa are minimal, and since the range of *D. membranacea* is not geographically continuous, we consider that this taxon should be viewed as a variety of *D. sessiliflora*.

***Dicoma sessiliflora* Harv. subsp. *sessiliflora* var. *membranacea* (S.Moore) S.Ortiz & Rodr.Oubiña, comb. et stat. nov.**

D. membranacea S.Moore in Bulletin de l'Herbier Boissier, sér. II, 4: 1025 (1904).

ACKNOWLEDGEMENTS

Many thanks to the curators of herbaria from which material has been loaned for the present study and to Guy Norman for the English translation.

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MS. received: 1996-02-01.

VITACEAE

A NEW SPECIES OF *RHOICISSUS* FROM THE EASTERN CAPE

***Rhoicissus kougabergensis* Retief & Van Jaarsv., sp. nov.**, *R. microphyllae* (Turcz.) Gilg & M.Brandt et *R. laetantis* Retief affinis, sed distributione et lamina folii ambitu anguste obovata, non ovata vel elliptica (ut in *R. microphylla*) nec elliptico-obovata (ut in *R. laetantis*) differt.

TYPE.—Eastern Cape, 3324 (Steytlerville): Kouga Dam, NW of chalets, (–DA), *Van Jaarsveld 13796* (PRE, holo.; E, G, K, MO, NBG, iso.).

Spreading shrub with tendency to scramble, covered with equally two-armed, unicellular hairs. *Roots* thick and fleshy. *Tendrils* absent. *Branches* with leaves aligned on one side; old bark greyish white, rough. *Leaves* simple, petiolate; blade narrowly obovate, (22–)30–55(–65) × (6–)10–22(–27) mm, entire, apex obtuse or slightly emarginate, thick in texture, discolorous with lower surface reddish brown, upper surface glaucous green or both surfaces more or less of the same colour, lower surface more densely hairy; base of blade cuneate or asymmetric; young leaves covered throughout with reddish brown hairs; older leaves pale white or transparent on upper surface; petiole 2–4(–7) mm long; stipules present, soon deciduous. *Inflorescences* leaf-opposed, ± condensed, reddish brown, bracteate, thyrsoid cymes. *Flowers* regular, bisexual, pedicellate, globose in bud; pedicels 0.5–1.0 mm long. *Calyx* 5-lobed, cup-shaped, ± 1 mm high; lobes broadly ovate. *Corolla*: petals 5, ovate, 1.5–2.0 mm long, greenish yellow. *Stamens* 5, opposite petals, bending over gynoecium; filaments 1 mm long; anthers dorsifixed. *Disc* entire with ovary immersed in it. *Style* simple, entire; stigma inconspicuous. *Fruit* a 1-seeded berry, globose, 8–10 mm in diameter, stalk ± 1.5 mm long (Figures 5 & 6).

The globose flower bud and the thick, entire disc of *Rhoicissus kougabergensis* indicate that it belongs to the genus *Rhoicissus* (Retief 1993). It is the fourth southern African member of the genus with simple leaves. All other known species have 3- or 5-foliate leaves. *R. kougabergensis* differs from *R. microphylla* in the outline of its leaves which are narrowly obovate (Figure 7A). Table 3

summarizes differences between the simple-leaved species known from southern Africa. The other three species with simple leaves can be distinguished as follows: 1, *R. microphylla* has ovate to elliptic leaves (Figure 7B) and equally two-armed, reddish brown, unicellular hairs (Figure 8), somewhat more slender than those of *R. kou-*

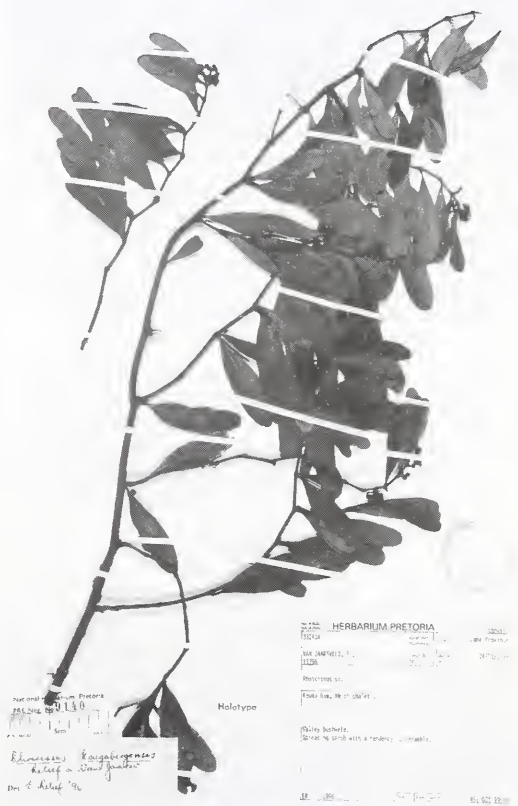


FIGURE 5.—Holotype of *Rhoicissus kougabergensis*, Van Jaarsveld 13796 (PRE).

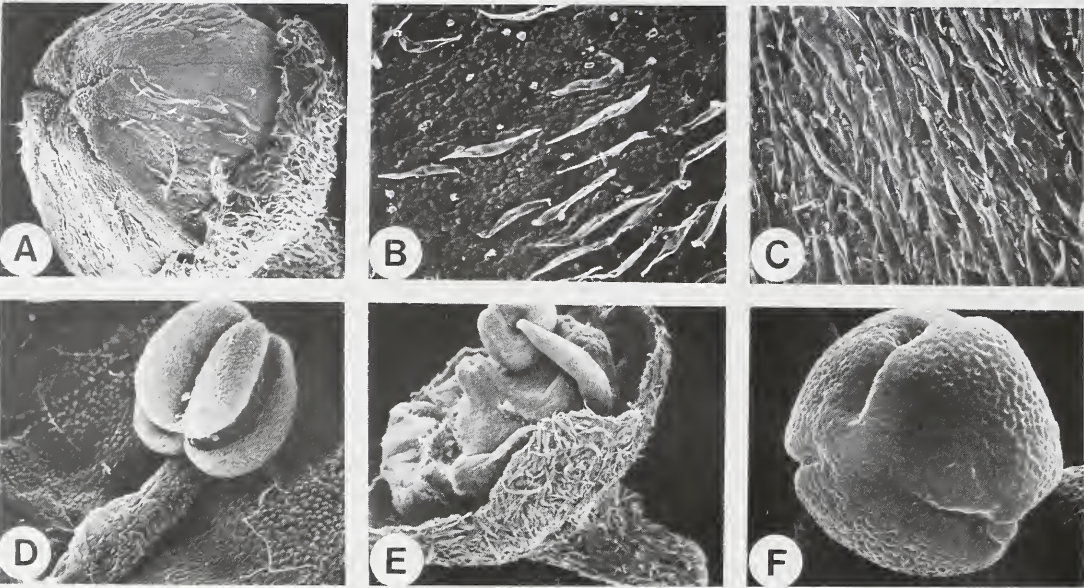


FIGURE 6.—*Rhoicissus kougabergensis* Retief & Van Jaarsv.: A, flower bud; B, upper surface of leaf; C, undersurface of leaf; D, stamen; E, stamen bending over gynoecium; F, pollen grain. SEM micrographs from Van Jaarsveld 13796. A, $\times 169$; B, $\times 53$; C, $\times 53$; D, $\times 40$; E, $\times 18$; F, $\times 1540$.

gabergensis, giving a rusty brown appearance to the species. *R. microphylla* occurs in the Queenstown-Cathcart area, whereas *R. kougabergensis* is found only in the vicinity of the Kouga Dam (Figure 9); 2, *R. laetans*, which has elliptic, glabrous leaves, is endemic to the Blydepoort Nature Reserve area in Mpumalanga (Figure 9); 3, *R. tomentosa* (Lam.) Wild & R.B.Drumm. has shallowly lobed, broadly transversely elliptic or reniform leaves and is a high-climbing liane in contrast to *R. kougabergensis*, a spreading shrub.

The pollen grains of *R. kougabergensis* are typically isopolar and radially symmetrical. In polar view the grains are triangular to circular; the mesocolpia are convex and the equatorial view is elliptic. The colpi are long, narrow and granular with pointed ends; the tectum is reticulate with densely spaced lumina (Figure 6F).

Rhoicissus kougabergensis is endemic to the Kouga Dam area (only locality known) within the Kouga-Baviaanskloof Wilderness Area in the southern Eastern Cape where it occurs on steep slopes (Figure 9). The vegetation in the region consists of subtropical thicket, domi-

nated by the spekboom, *Portulacaria afra* Jacq., with fynbos on the upper slopes. The climate is hot in summer and mild in winter. The rainfall varies between 300 and 400 mm annually and occurs in summer and winter, but the winters tend to be drier. The terrain is rugged and the acid, quartzitic, sandstone soils are poor in minerals. According to Archer & Van Wyk (1993), *R. digitata* (L.f.) Gilg & M.Brandt, *R. revouilii* Planch. and *R. tridentata* (L.f.) Wild & R.B.Drumm. subsp. *tridentata* occur in the Kouga-Baviaanskloof Wilderness Area. *R. kougabergensis* with simple leaves is easily distinguished from these species which all have 3- or 5-foliolate leaves. *R. kougabergensis* starts flowering \pm in October.

The Kouga-Baviaanskloof Wilderness Area does not appear to contain an exceptionally rich flora, nor is it very rich in endemic species. The area is still undercollected and future floristic surveys will undoubtedly add many new records and even new taxa (Archer & Van Wyk 1993). Some endemic species occurring in the vicinity of *R. kougabergensis* include two tree species, *Sterculia alexandri* Harv. and *Atalaya capensis* R.A.Dyer. Smaller endemic species include *Aloe pictifolia* D.S.Hardy, *Gasteria*

TABLE 3.—Southern African species of *Rhoicissus* with simple leaves

Species	Leaf shape	Hairs	Habit	Distribution
<i>R. kougabergensis</i>	narrowly obovate	reddish brown or transparent, equally 2-armed, unicellular	spreading shrub	endemic to Kouga Dam area, Eastern Cape
<i>R. microphylla</i>	ovate to elliptic	as in <i>R. kougabergensis</i> , but more slender	small shrub	Queenstown-Cathcart area, Eastern Cape
<i>R. laetans</i>	elliptic	absent	shrub	endemic to Blydepoort area, Mpumalanga
<i>R. tomentosa</i>	shallowly lobed, broadly transversely elliptic or reniform	long, thin, unicellular	high-climbing liane	forests and woodland of the Northern Province, Mpumalanga and Swaziland; coastal dune forests of Kwazulu-Natal and Eastern Cape.

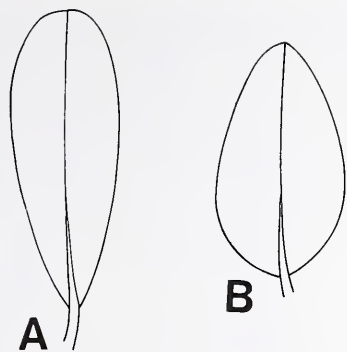


FIGURE 7.—Characteristic leaf blade outlines of: A, *Rhoicissus kougabergensis*; B, *R. microphylla*, $\times 1$.

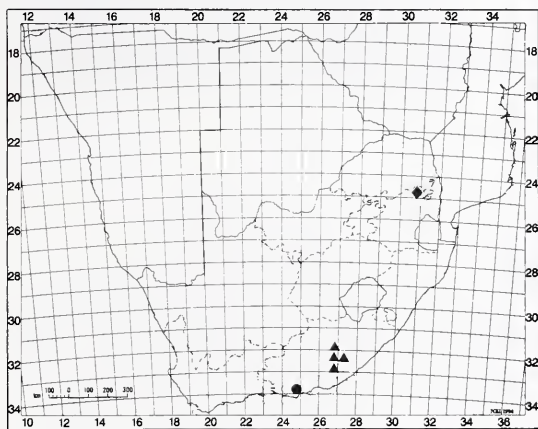


FIGURE 9.—Known distribution of *Rhoicissus kougabergensis* Retief & Van Jaarsv., ●; *R. microphylla* (Turcz.) Gilg & Brandt, ▲; *R. laetans* Retief, ◆.

glomerata Van Jaarsv. and *G. ellaphieae* Van Jaarsv., *Cyrtanthus flammulosus* Snijman & Van Jaarsv. and *C. labiatus* R.A.Dyer.

EASTERN CAPE.—3324 (Steytlerville): Kouga Dam, sheer slope above wall, (–DA), *Van Jaarsveld* 9902 (NBG, PRE); Kouga Dam, NW of chalets, (DA), *Van Jaarsveld* 13796 (E, G, K, MO, NBG).

ACKNOWLEDGEMENTS

The authors wish to thank Mr Rob Welsh for his help in searching for fruits at the Kouga Dam.

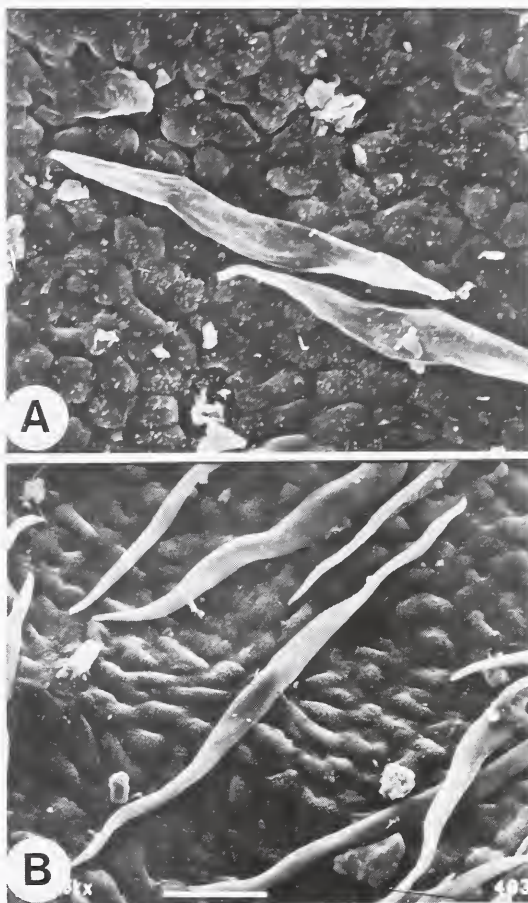


FIGURE 8.—SEM micrographs of upper surface of leaf with two-armed hairs: A, *Rhoicissus kougabergensis*, $\times 234$; B, *R. microphylla*, $\times 198$.

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 MS. received: 1996-05-10.

APIACEAE (UMBELLIFERAE)

A NEW NAME FOR A SOUTH AFRICAN *PEUCEDANUM*

Conservation of the name *Peucedanum capense* (Thunb.) Sond. (1862) against *P. capense* (Eckl. & Zeyh.) D.Dietr. (1840) was proposed some years ago (Burt 1989; 1991: 271). Under the Code then current this might have been a contentious case, and the Committee for Spermatophyta therefore decided

to postpone its decision until after the Tokyo Congress, when changes to that part of the Code were expected. These were, indeed, made and the retention of *Peucedanum capense* (Thunb.) Sond. has been approved by the Committee [votes 12:0—see *Taxon* 45: 671 (1996)].

There remains the question of the correct name for the rejected *P. capense* (Eckl. & Zeyh.) D.Dietr., which is currently known as *P. multiradiatum* Drude. That name, however, is illegitimate. Under the Tokyo Code it would be possible to propose *P. multiradiatum* for conservation, but *P. multiradiatum* is a much less common plant than *P. capense* (Thunb.) Sond. and I am not alone in thinking that conservation in this case is unwarranted. A change of name will cause only a tiny ripple in South African plant nomenclature and a proposal for conservation means further work for the Committee, further delay in a final decision, and no certainty that conservation would eventually be granted. A simple name change now will close the issue, and the following new name is therefore established:

***Peucedanum polyactinum* B.L.Burt, nom. nov.**

Type.—Cape, Stellenbosch, Klampmuts, *Ecklon & Zeyher* 2239 (S).

Oreoselinum capense Eckl. & Zeyh., Enumeratio plantarum africae australis extratropicae: 350 (1837). *Peucedanum capense* (Eckl. & Zeyh.) D.Dietr.: 967 (1840), non *P. capense* (Thunb.) Sond. nom. conserv. *Bubon multiradiatum* E.Mey. in Drège: 169 (1843) nom. nud. *Bubon capense*

(Eckl. & Zeyh.) Sond.: 561 (1862). *Peucedanum multiradiatum* Drude: 237 (1898), nom. illegit.

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 MS. received: 1996-10-28.

PROTEACEAE

A NEW SPECIES OF *LEUCADENDRON* FROM THE WESTERN LITTLE KAROO

This large distinctive *Leucadendron* was unknown in South African herbaria until specimens collected by Mr David Osborne of the Cape Dept of Nature Conservation, Ladismith, were submitted for identification in 1994. Prior to that it had been observed at several sites on Anysberg at the western end of the Little Karoo in the Western Cape by officers of the Cape Dept of Nature Conservation although the taxonomic status of these populations was uncertain.

Subsequent field studies have established that it is fairly widely dispersed at the western end of the Klein Swartberg and Little Karoo. It is here described as new and commemorates David Osborne, who made the first recorded herbarium collections of this species and whose thorough collecting for the Protea Atlas Project has greatly increased our knowledge of the Proteaceae in the Little Karoo region.

***Leucadendron osbornei* Rourke sp. nov.**

Frutex erectus robustus ad 4 m altus, *Leucadendroni teretifolio* affine, sed statura grandiore, foliis glabris acerosoteteritibus 15–28 mm longis, inflorescentiis masculinis 20–35 mm longis, et strobilis femineis maturis 30–40 mm longis differt.

TYPE.—Western Cape, 3320 (Montagu). Witteport, extreme western end of Klein Swartberg, (–BD), 9-11-1995, J.P. Rourke 2110 (NBG, male specimen, holo.!, BOL, K, MO, NSW, PRE, S, iso.!).

Robust rigid shrub 1.5–4.0 m tall with a stout main trunk to 75 mm in diam. Branches stiffly erect, rigid, glabrous, 5–10 mm in diam. Leaves acicular terete, 15–28 × 1.5–2.0

mm, ascending, hard and cartilaginous, glabrous, slightly glaucescent, upper surface minutely canaliculate; slightly shorter in male plants. Male inflorescences densely clustered in groups of 8 to 16 on short (30–60 mm long) branchlets on flowering shoots. Inflorescence cylindric, 20–35 × 10 mm, pedunculate; peduncle 10 × 2 mm, sparsely sericeous, covered with tightly adpressed subulate bracts 2–3 mm long, glabrous, but margins ciliate. Floral bracts ovate, 1 × 1 mm, tightly clasping perianth, glabrous but margins ciliate. Perianth sessile, 5–6 mm long, straight, glabrous, bright yellow; perianth claws equally recurved at anthesis; tube cylindrical. Anthers 4; pollen powdery. Style filiform, 6 mm long, glabrous. Pollen presenter clavate-acute, 1 mm long. Hypogynous scales 2 mm long, projecting to top of tube. Female inflorescences free-standing, surrounded by a loose pseudowhorl of patent involucreal leaves, greenish ivory to yellow at anthesis. Flowering cone ovoid-clavate, obtuse, 30–40 × 12–14 mm, shortly pedunculate; peduncle 10–15 × 10 mm. Involucreal bracts dark brown, very narrowly lanceolate-acuminate to subulate, 8–12 × 1.5 mm, tightly adpressed to peduncle, glabrous but margins ciliate. Floral bracts broadly ovate, acute, 3 × 5 mm, glabrous. Perianth 3 mm long, laterally compressed; tube region 2 mm long, densely sericeous; claws and limbs recurved, glabrous. Staminodes generally 3, anterior staminode usually absent. Style glabrous, 5 mm long, slightly abaxially deflexed in upper half. Ovary ovoid to spherical, glabrous, 1 mm long. Pollen presenter minutely capitate, inconspicuously bilobed with glandular hairs on the abaxial face. Hypogynous scales ovate-acute, 1 mm long. Mature female cone ovoid-acute, 35–60 × 25–30 mm, brown, becoming silvery grey with age. Fruit a flattened black samara, 70 × 50 mm, apically retuse (Figure 10).



FIGURE 10.—*Leucadendron osbornei*: A, young female cones and a mature fruiting cone; B, branches on an old female plant showing serotinous cones retained for up to eight years; C, David Osborne next to a mature female plant; D, densely clustered male inflorescences. B, C, & D taken at type locality, Witteport, Klein Swartberg

Diagnostic characters

Apart from the obvious differences in the size and stature of the mature shrubs, *L. osbornei* is distinguished from *L. teretifolium* by its longer leaves, 15–28 mm long; longer male inflorescences, 20–35 mm long and by the much longer (35–60 mm long) mature female cones. In *L. nobile* the male inflorescences are produced more sparsely in

smaller numbers. The male inflorescences in *L. nobile* (30–70 mm long) are very much larger than in *L. osbornei*, whereas the male flowers are loosely arranged in a lax spike and are pubescent basally in the tube region. The male flowers in *L. teretifolium* usually have a bright red spot at the apex of each bud but in both *L. osbornei* and *L. nobile* they are uniformly yellow (Table 4).

Key to species

TABLE 4.—Differences in leaf and inflorescence dimensions between *L. osbornei* and related species

	Leaf length (mm)	Length of male inflorescence (mm)
<i>L. nobile</i>	41–58	30–70
<i>L. osbornei</i>	15–28	20–35
<i>L. teretifolium</i>	8–22	5–10

- 1a Male inflorescences globose, 5–10 mm long; mature female cones up to 35 mm long *teretifolium*
- 1b Male inflorescences cylindric, 20–90 mm long, mature female cones 30–90 mm long:
- 2a Male flowers completely glabrous; male inflorescences numerous, 20–35 mm long, clustered together on short branchlets; Western Cape, western Little Karoo . . . *osbornei*
- 2b Male flowers minutely pubescent in tube region; male inflorescences solitary, 30–70 mm long, sparsely produced; Eastern Cape, Kouga, Baviaanskloof & Willowmore Mountains *nobile*

Affinities

Leucadendron nobile Williams, *L. teretifolium* (Andr.) Williams and the species here described as *L. osbornei* Rourke form a well-defined group within *Leucadendron* subsection *Compressa*, characterised by their uniformly acicular glabrous leaves and glabrous cones.

The robust vegetative growth, large stature of the mature shrub and impressive size of the mature female cones in *L. osbornei* initially suggested an affinity with *L. nobile*, a species from the Humansdorp, Willowmore and Steytler-ville Districts of the Eastern Cape. However, in the morphology, arrangement and number of male inflorescences, *L. osbornei* is clearly more closely allied to *L. teretifolium* than to *L. nobile*. In both *L. teretifolium* and *L. osbornei* the male plants are covered with masses of male inflorescences on short branchlets borne at the ends of flowering shoots, and in both species the male flowers are completely glabrous and borne in tightly congested cylindric inflorescences. This is unlike *L. nobile* where the male inflorescences are relatively sparsely produced on the ends of long shoots.

At one locality, a site south of trig. beacon 66 on Matjiesgoedberg, *L. osbornei* and *L. teretifolium* occur sympatrically (2–3 m apart), with no evidence of hybridization. From observations made at this site, it appears that there is little or no overlap in their flowering periods. During a site visit on 5–11–1996, *L. teretifolium* was observed to be nearly past its flowering period while *L. osbornei* was still in bud, about two weeks from flowering.

Significantly, the male flowers in both species produce quite different odours which may attract different pollinators. The male flowers in *L. teretifolium* give off a sweet, slightly lemon-scented odour with faint sulphurous undertones while in *L. osbornei* they produce a smell reminiscent of fresh human semen. Prominent nectar droplets form at the base of the male flowers in *L. osbornei* which attract large numbers of *Diptera* during the day when the air temperature reaches about 25°C. I have not observed potential pollinators on *L. teretifolium*. Both Williams (1972) and Rebelo (1995) note that *L. teretifolium* produces showers of pollen when shaken, indicating that it is wind-pollinated.

Distribution and habitat

This species is restricted to mountains at the western end of the Little Karoo in the southwestern Cape at elevations between 700 and 1 500 m. Populations of *L. osbornei* occur on Elandsberg north of Sevenweeks Poort at its northeasterly limits; the western end of the Klein Swartberg at Wittepoort and Paardenfontein; the north-eastern corner of Touwsberg; on Anysberg; on Matjiesgoedberg north of Anysberg at the western end of its range and on Rooiberg near the Floriskraal dam. *Leucadendron osbornei* occurs mainly in Dry Mountain Fynbos or in the ecotone between Dry Mountain Fynbos and Karroid Broken Veld (Acocks 1988) or between Dry Mountain Fynbos and Central Mountain Rhenosterveld (Moll *et al.* 1984). Most of the known localities are on Witteberg Quartzite and a few are on Table Mountain Sandstone (Figure 11).

These localities are generally extremely arid, receiving a mean annual rainfall of between 150 and 200 mm. *Merxmuellera arundinacea* and *Erica spectabilis* are commonly associated species.

In several populations many of the shrubs observed were between 3 and 4 m in height. The females are almost invariably slightly taller than the males. Vegetative growth in such habitats is slow, and attempts to count annual vegetative growth increments indicated that such specimens were in excess of 50 years old. *Leucadendron osbornei* is strongly serotinous, retaining unopened cones for up to seven and eight years (Figure 12). Flowering takes place from early to late November depending on site aspect.

Conservation status

The exact conservation status of this species is not clear as the known populations have not yet been adequately assessed. Most populations which I have observed consist of about 100 or fewer mature individuals. It is probably best described as naturally rare but under no obvious man-made threat at present. The Matjiesgoedberg and Anysberg stands are protected within the Anysberg Nature Reserve administered by the Cape Dept of Nature Conservation.

Specimens examined

WESTERN CAPE.—3320 (Montagu): Matjiesgoedberg, above Matjieskloof on South side below trig. beacon 66, (–BC), Nov., *Rourke 2114* (NBG); Anysberg, 3.8 km west of trig. beacon 66 on Farm Matjieskloof, (–BC), March 1994, *Osborne 94022302* (NBG); Wittepoort, western end of Klein Swartberg above Kromkloof, (–BD), March 1995, *Rourke 2071* (NBG); Rooiberg, Driehingskloof, westernmost part of peak on Laingsburg-Prince Albert road, 7–11–1994, *Osborne s.n.* (NBG). 3321 (Ladismith): Touwsberg, on Farm Basseur, (–CA), 23–9–1994, *A. September 94092301* (NBG); Elandsberg, on Ylanskloof 211, 0.8 km from spot height 1533, (–AD), 13–11–1995, *K. Mars 95111303* (NBG).

ACKNOWLEDGEMENTS

I am most grateful to Mr David Osborne, Cape Dept of Nature Conservation, Ladismith, who arranged several

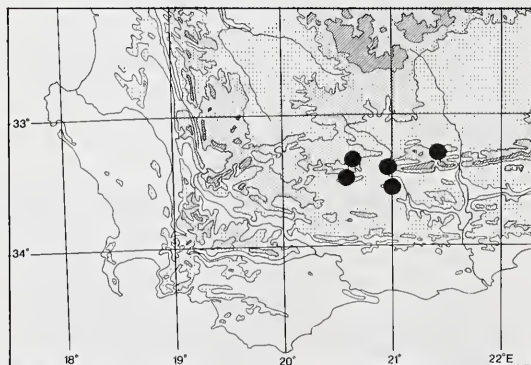


FIGURE 11.—Distribution of *L. osbornei*.

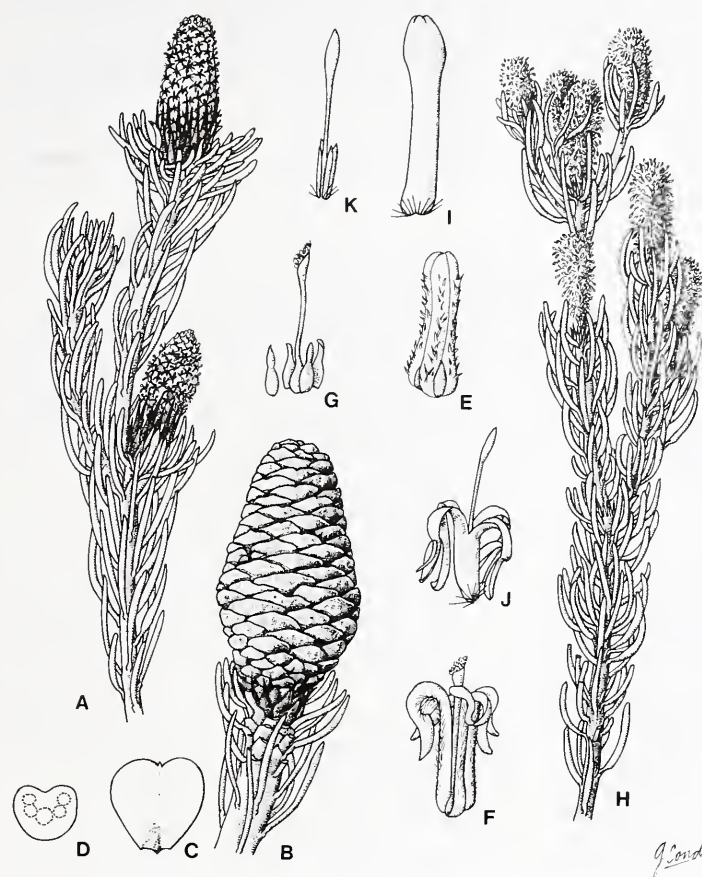


FIGURE 12.—*Leucadendron osbornei*. A, female inflorescences in flower, $\times 0.7$; B, mature female cone, $\times 0.7$; C, seed, $\times 2.3$; D, section through leaf, $\times 5.4$. E–G, female flower, $\times 5.4$: E, in bud; F, open; G, gynoecium with hypogynous scales. H, shoot with male inflorescences, $\times 0.7$. I–K, male flower, $\times 5.4$: I, in bud; J, open; K, showing pollen presenter and hypogynous scales.

field excursions which enabled me to examine this species at various localities within its distribution range and to Dr Ion Williams who read and reviewed the manuscript.

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MS. received: 1996-12-11.

BORAGINACEAE

THE TAXONOMIC STATUS OF *LOBOSTEMON HORRIDUS*

Levyns (1934) in describing *L. horridus* Levyns, lists a *Levyns 2881* collection. She did not, however, personally collect this material as it is clear from the particular herbarium label that J. Rennie was the collector. Levyns based her description on two herbarium specimens available to her, namely *Compton 2971* (BOL) and *J. Rennie s.n. sub Levyns 2881* (BOL, STE). Subsequent collections have been few and far between. A total of four collections,

the last being *Acocks 23698* (PRE) in 1965, had been made at the onset of the current revision of the genus. The aforementioned scarcity of collections resulted in *L. horridus* being included in the *Red Data List of southern African plants* (Hilton-Taylor 1996). All attempts to recollect the taxon at the type locality have failed. The most recent collection close to the type locality has been *M.H. Buys 523* at Pienaarskloof, about 40 km northwest of Mat-

jiesfontein. Examination of all available herbarium specimens as well as field work led us to suspect that *L. horridus* and *L. paniculatus* are conspecific.

According to the diagram presented by Levyns (1934: 412), *L. paniculatus* and *L. horridus* are closely related. Although Levyns provides no summary of differing characters in her diagnosis of *L. horridus*, one can catch a glimpse at what her thoughts might have been through her choice of the specific epithet. The herbarium specimens at her disposal both exhibit leaves with an extremely spinous indumentum. The current revision has confirmed that leaf characters based on the indumentum are unreliable for systematic purposes. Levyns (1934) warns against the undue use of morphological characters in *Lobostemon*, yet leaf shape and indumentum type distinguish *L. paniculatus* from *L. horridus* in her key.

A critical comparison of characters between *L. paniculatus* and *L. horridus* reveals no significant diagnostic differences between them. The difference in hairiness of the leaves, the pronounced midrib and thickened margins are ascribed to arid habitats. The less spiny forms (= *L. paniculatus*) are generally to be found near water in and amongst the larger mountain ranges of the Swartberg. The spiny forms (= *L. horridus*) become more abundant as one proceeds further into the interior of South Africa. The variation allowed here in the indumentum with the sinking of *L. horridus* is no greater than that allowed for in *L. echiioides* for example.

L. paniculatus and *L. horridus* share the following character states to the exclusion of the other members of the section *Lobostemon*: 1, adaxial surface of young leaves appearing glabrous, becoming hairy with age; 2, possession of two distinct trichome lengths; 3, two corolla lobes slightly larger than the rest; 4, hairs on the abaxial side of the corolla lobes largely confined to the midveins (this differs markedly from *L. echiioides* where the hairs are confined to the distal parts of the lobes); 5, identical fruit structure.

It is for the above reasons that *L. horridus* Levyns is viewed to be conspecific with *L. paniculatus*. The nomenclatural history of *L. paniculatus* therefore reads as follows:

***Lobostemon paniculatus* (Thumb.) Buek** in *Linnaea* 11: 139 (1837); DC.: 8 (1846); C.H. Wright: 33 (1904); Levyns: 418 (1934). Type: Cap. b. Spei, *Thunberg s.n. sub UPS 4109* (UPS, holotype!).

Echium paniculatum Thunb.: 33 (1794); Willd.: 784 (1798); Pers.: 163 (1805); Schrad.: 41 (1806); Poir.: 675 (1808); Thunb.: 9 (1811); Lehm.: 425, 473 (1818); Roem. & Schult.: 11 (1819); Lehm.: t. 23 (1823); Thunb.: 165 (1823).

Lobostemon horridus Levyns: 419 (1934). Type: Whitehill near Matjiesfontein, J. Rennie s.n. sub Levyns 2881 (BOL, lectotype; STE, isotype!).

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 MS. received: 1996-12-02.

Composition and biogeography of forest patches on the inland mountains of the southern Cape

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Keywords: biogeography, corridors, evergreen forest, geomorphology, rare species, species-area relationship

ABSTRACT

Patterns in species richness of 23 small, isolated forests on the inland mountains of the southern Cape were studied. Species richness of woody plants and vines of the Kouga-Baviaanskloof Forests was higher than in the western mountain complexes, where species richness in the more southern Rooiberg and Kamanassie Mountains was higher than in the Swartberg range. The Rooiberg, a dry mountain with small forests far away from the coastal source area, had more species than, and contained many species which are absent from, the larger, moister forests of the Kamanassie which are closest to the coastal source areas. Neither altitude nor distance from the source area, the forests south of the coastal mountains, nor long-distance dispersal, adequately explained the variation in species richness. The variations are best explained in terms of dispersal corridors along the Gouritz and Gamtoos River systems which connect the coastal forests with the inland mountains. The distribution patterns of four species groups in relation to the geomorphological history of the two river systems provide relative dates for the expansion and contraction of temperate forest, subtropical forest and subtropical transitional thicket in the southern Cape.

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1 INTRODUCTION

In the southern Cape several mountain complexes occur north (inland) of the coastal mountains. These inland mountains are surrounded by semi-arid to arid valleys and lowland. Two river systems, however, connect the inland areas with the coast. A third river system almost breaks through the coastal mountains near one of the inland mountains. Forests on the inland mountains are very small and isolated and are in sharp contrast to the large and widespread forests along the coast (Anon. 1987). Their distribution, composition and conservation status are poorly known.

Axelrod & Raven (1978) and Deacon (1983) reconstructed the palaeofloras of Africa. They speculated that the temperate forest which covered the southern tip of Africa during the Palaeocene (65 to 55 My BP) was replaced by subtropical forest during the Oligocene-Miocene (37 to 5 My BP) and subsequently by fynbos and arid shrublands during the Late Pleistocene (125 000 to 10 000 yBP). The general increasing aridity in the southern Cape region since the beginning of the Miocene (24 My BP) (Deacon 1983) suggests further that over time the inland forest patches became increasingly isolated. Hypothetically the current flora of the isolated inland forests would therefore consist of species which have survived in suitable refuge sites, species with tolerance ranges which would enable them to survive in the changed environment, and species which have colonized from suitable forest source areas. Geldenhuys (1986; 1992a, b; 1994) studied several aspects of the distribution, fragmentation and biogeography of the South African forests in general and the southern Cape coastal forests in particular. The question was raised: how do the inland forests relate to the coastal forests in the southern Cape? Several studies have successfully used geomorphological evidence to reconstruct the biogeography of floras and taxa (Kaul *et al.* 1988; Moore 1988) and the phylogeny of families and genera, e.g. of freshwater fishes (Skelton 1986). Smith (1981) considered the geological and palaeogeographical

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MS. received: 1996-02-08.

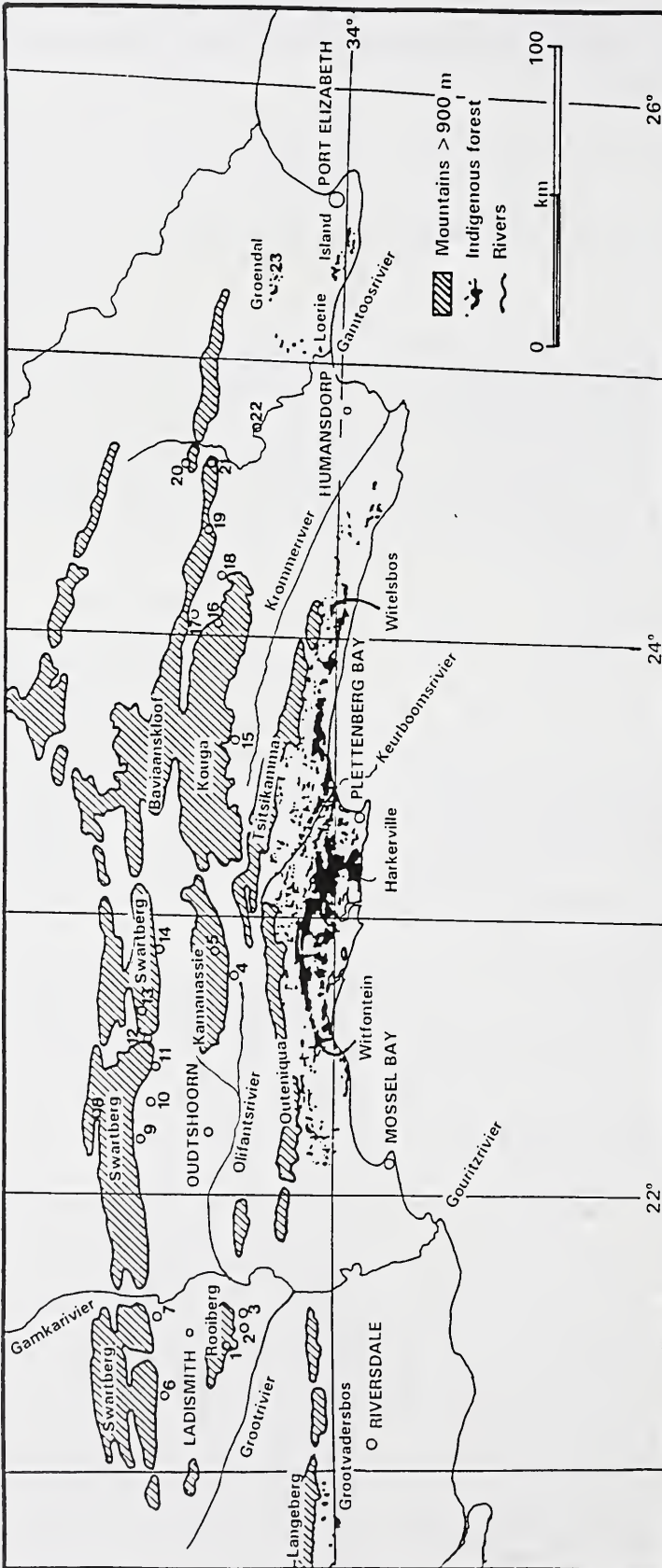


FIGURE 1.—The study area of the southern Cape inland mountains in relation to the widespread forests south of the coastal ranges. The numbers represent the following study sites in the respective mountain complexes (the forests are too small to be indicated on the map): Roodberg: 1, Bosrivier upper; 2, Bosrivier lower; 3, Assegaaibosrivier; Kannaassie: 4, Klusrivier; 5, Meulrivier upper; Swartberg: 6, Waterkloof; 7, Seweweekspoort; 8, Swartbergpoort; 9, Swartberg Pass; 10, Rust-en-Vrede; 11, Huisrivier upper; 12, Meiringspoort; 13, Tienkloof; 14, Cheridouwspoor. Kougga: 15, Saptevriervier. Baviaanskloof: 16, Doringkloof; 17, Diepnekklouf; 18, Geelhoutbos; 19, Assegaaikloof; 20, Witvriervierpoort; 21, Witvriervierpoort; 22, Grootvriervierpoort; 23, Zungarivier.

history of the landmasses around Tasmania as well as colonizing ability and altitudinal range of species in a study of the origin of the Tasmanian high mountain flora.

Taxa move from source areas along different pathways (corridors, filters or sweepstake routes) to colonize new sites (Brown & Gibson 1983). If they move along a corridor (which contains a wide variety of suitable sites or habitats), the composition of the community in the new site will be very similar to the community at the source. If they move through a filter (which contains a limited variety of suitable sites or habitats), the community at the new site will contain a limited component of the source community. If they move along a sweepstake route (which cuts across areas with totally different environments), the community in the new site will contain only species which will survive long distance dispersal across unsuitable areas. Island biogeographic theory was evoked to explain the extinction and colonization of animal species on oceanic islands of different size and distance away from the source areas (MacArthur & Wilson 1967), and more recently for plants in islands of fynbos in the southern Cape forests (Bond *et al.* 1988). Dispersal is only of significance if the organism can establish a viable population upon arrival in the new area (Brown & Gibson 1983). Physical and biological barriers to successful colonization by forest plants are insufficient moisture (arid valleys), extreme temperature (mountain tops, frost in valleys), disturbance patterns (fire in fynbos) and absence of long distance dispersal agents (migrant frugivorous birds). However, man-induced changes in the vegetation and environment during historical times may eliminate or confuse the evidence required to elucidate the biogeographical patterns.

The objectives of this study were:

- to determine the patterns in species composition and richness of forest communities in different inland mountain complexes of the southern Cape.
- to explain the observed patterns in terms of habitat preferences of species; species-area and species-distance relationships; long-distance dispersal; dispersal corridors in relation to the geomorphological history of the landscapes in the region.
- to aid interpretation of vegetation changes in the coastal forests from the dating of forest expansion and contraction on the inland mountains.

2 STUDY AREA

The study covers the Cape Folded Belt in the southern Cape of South Africa, between Ladismith and Riversdale in the west and Humansdorp in the east (Figure 1). A site in the Groendal Wilderness Area northwest of Port Elizabeth was included as a riverine site in the coastal mountains which appeared to be similar to the sites in the inland mountains. The dominant physiographic feature of the main study area are the subparallel mountain ranges and the intermontane lowland belts which run approximately east-west (Lenz 1957). In the west the Swartberg range, the highest range in the study area (up to 2 250 m) forms the northern boundary. The Kouga-Baviaanskloof Mountain complex forms the northern boundary to the east. It consists of several parallel ranges with relatively narrow

east-trending valleys. The coastal Langeberg-Outeniqua-Tsitsikamma ranges form the southern boundary. A number of smaller, almost isolated mountains occur between the Swartberg and the Langeberg-Outeniqua ranges: Rooiberg-Gamka Hill between Calitzdorp and Ladismith, and Kamanassie Mountain between Oudtshoorn and Uniondale. The Oudtshoorn basin is a large semi-arid lowland between the Swartberg, Rooiberg, Outeniqua and Kamanassie Mountains which comprises hills of Cretaceous conglomerates (Lenz 1957). The relatively narrow Langkloof valley separates the Tsitsikamma Mountains from the Kouga Mountains. Groendal is a hilly landscape between the Great Winterhoek and Elandsberg Mountains. A relatively dry coastal plain occurs to the southeast of Groendal.

Three river systems link, or partially link, the coastal area with the inland mountains and are important for the interpretation of the forest flora. The Gouritz River breaches the Langeberg-Outeniqua ranges west of Mossel Bay through the Gouritzpoort. Inland it is formed by the confluence south of the Rooiberg of the Olifants River which drains the Oudtshoorn basin, the Gamka River which flows through the Swartberg north of Calitzdorp and which drains the Karoo west of Beaufort West, and the Groot River which drains the area to the west of the Rooiberg. Tributaries of these rivers breach the Swartberg range through several poorts such as, from west to east, Seweweekspoort, Gamkapoort, Meiringspoort and Cheri-douwspoort. A poort is a relatively narrow, steep-walled opening, cutting almost perpendicularly across a topographic barrier, through which the open areas on either side are connected, usually by a river (Lenz 1957). The Keurbooms River which runs between the Kamanassie Mountain and Plettenberg Bay, does not fully breach the gap between the Outeniqua and Tsitsikamma ranges south of the Kamanassie Mountain. A low, narrow ridge separates its origin from the Kamanassie River which drains the southern slopes of the Kamanassie Mountain and runs in a northwesterly direction to join the Olifants River. The Gamtoos River east of Humansdorp is formed by the confluence of the Baviaanskloof and Groot Rivers. The Witrivier is a small stream which joins the Groot River north of the Grootrivierpoort at Cambria. The Zunga (or Swartkops) River runs from Groendal towards the coast at Port Elizabeth.

Geologically the mountains owe their existence to their heavily folded structure and the resistance of the quartzitic Table Mountain Sandstones to weathering. Softer sandstones and shales of the Bokkeveld Series eroded more readily to form the syncline valleys (Lenz 1957; Theron 1962; Toerien 1979).

The few weather stations in the area all occur in the lowlands. Data are available for short periods for a number of rain gauges across the Swartberg (along the Pass and in the east) and Kamanassie Mountains. Rainfall increases linearly with increase in elevation, and rain shadow effects are apparent on north slopes. In the Swartberg Pass area annual rainfall declines rapidly from 725 mm at 1 600 m to 210 mm at 884 m on the northern foothills and to 182 mm at 686 m in Prince Albert on the edge of the Great Karoo (Bond 1981). Annual rainfall on the southern foothills is 411 mm at 640 m (Cango Caves)

and 570 mm at 762 m (Rust-en-Vrede, forest site No. 10, Figure 1, Table 1) (Weather Bureau 1986 unpubl.). In Swartberg East, near Blesberg between the Tierkloof and Cheridouwspoor sites (Nos 13 & 14 respectively), annual rainfall ranged from 766 mm on the northern midslope, to 847 mm on the crest, 798 mm on the upper south slope and 572 mm on the southern foothills (unpublished data). In the Kamanassie annual rainfall near the crest ranged between 815 mm on the southern side and 682 mm on the northern side, and declined to 239 mm on the southern foothill and 169 mm on the northern foothill (Kamanassie Policy Memorandum, Department of Nature Conservation). Rainfall data for Rooiberg are unreliable but appear to be lower than for the Kamanassie, also as judged from the appearance of the fynbos vegetation on the southern slopes. Rainfall in the lowlands ranges between 220 mm at Van Wyksdorp (305 m) on the southern footslopes of the Rooiberg, 244 mm at Oudtshoorn (335 m), 482 mm at Joubertina (544 m) in the Langkloof, 321 mm at Studtis (760 m) in the western end of Baviaanskloof, and 536 mm on the southern foothills of Groendal (229 m; forest site No. 23) (Weather Bureau 1986 unpubl.).

Reliable information on temperature regimes is less available. Diurnal and seasonal temperature variation is large. Mean maximum temperature for the warmest month is 31.8°C for Oudtshoorn and 27.8°C for Uitenhage and the mean minimum temperature for the coldest month is 3.5°C and 5.8°C for the two towns respectively. The mean number of days per annum with frost is 7.3 and 1.4 for the two towns (Weather Bureau 1986). Snow occurs five or six times per annum on the Swartberg and may lie for more than two weeks (Bond 1981).

The main vegetation types of the area have been described by Acocks (1988), Taylor (1979), Bond (1981) and Cowling (1984), and in unpublished reports. Moun-

tain fynbos and grassy fynbos cover most of the mountains and are interspersed with small patches of evergreen forest in protected gullies and valleys. Karroid broken veld covers the low-lying valleys of the Little Karoo, and subtropical transitional thicket extends south of Groendal and occurs in parts of Baviaanskloof.

3 METHODS

Twenty-three forested gorges, gullies and riverine sites were visited to represent the variety of sites with forest species encountered on the inland mountains (Figure 1; Table 1). In this study the definition of a forest (Geldenhuys *et al.* 1988) was extended to accommodate scattered bush clumps and isolated trees of species which are usually associated with forest, as observed in Seweweekspoort, Meiringspoort and Cheridouwspoort. For each study site a list was compiled of all plant species which were associated with the forest communities. Emphasis was placed on recording all tree and shrub species, but taxa of other growth forms were also recorded as completely as possible.

The size of each forest (Table 1) was estimated in the field. Most forests consisted of a long, narrow stand along a stream or river. The length of the stream which was covered in the survey was estimated from 1 : 50 000 topographic maps and the mean width of the forest was estimated in the field. Altitude was read from the relevant 1 : 50 000 topographic maps.

Obvious or important disturbance factors affecting the forest communities were recorded. These included fire, flooding of rivers, landslides and wind.

TABLE 1.—List of forested sites visited in the inland mountains of the southern Cape

No.	Mountain	Forest site	Grid reference	Altitude, m	Forest area, ha	Forest habitat
1	Rooiberg	Bosrivier upper	33°41'S 21°30'E	500	20	Closed/open gorge, riverine/slopes, south
2	Rooiberg	Bosrivier lower	33°43'S 21°30'E	330	10	Closed/open gorge, riverine, south
3	Rooiberg	Assegaaibosrivier	33°43'S 21°34'E	300	40	Closed/open gorge, riverine, south
4	Kamanassie	Kluesrivier	33°39'S 22°48'E	980	120	Closed/open gorge, riverine/slopes, south
5	Kamanassie	Meulrivier upper	33°38'S 22°53'E	1 100	80	Closed/open gorge, riverine/slopes, south
6	Swartberg	Waterkloof	33°27'S 21°17'E	700	10	Closed/open gorge, riverine, south
7	Swartberg	Seweweekspoort	33°25'S 21°24'E	650	20	Open gorge, riverine
8	Swartberg	Swartbergpoort	33°19'S 22°04'E	950	5	Open/closed gorge, riverine, north
9	Swartberg	Swartberg Pass	33°21'S 22°05'E	1 300	3	Closed gorge, riverine, south
10	Swartberg	Rust-en-Vrede	33°24'S 22°21'E	850	15	Closed gorge, riverine/slopes, south
11	Swartberg	Huisrivier upper	33°25'S 22°29'E	1 170	10	Closed valley, riverine, south
12	Swartberg	Meiringspoort	33°25'S 22°34'E	600	30	Open gorge, riverine/slopes
13	Swartberg	Tierkloof	33°24'S 22°39'E	1 200	2	Closed/open gorge, riverine, north
14	Swartberg	Cheridouwspoort	33°27'S 22°54'E	720	10	Closed valley, open gorge, riverine
15	Kouga	Sapreerivier	33°40'S 23°36'E	580	30	Closed valley, open gorge, riverine/slopes
16	Baviaanskloof	Doringkloof	33°37'S 24°03'E	650	80	Closed gorge, riverine, north
17	Baviaanskloof	Diepnekkloof (Bosrug)	33°33'S 24°04'E	600	40	Closed/open gorge, riverine, south
18	Baviaanskloof	Geelhoutbos	33°38'S 24°15'E	300	20	Closed/open gorge, riverine/slopes, north
19	Baviaanskloof	Assegaaikloof	33°39'S 24°22'E	280	20	Closed/open gorge, riverine, south
20	Baviaanskloof	Witrivierkloof upper	33°36'S 24°31'E	1 170	2	Closed gorge, riverine, south
21	Baviaanskloof	Witrivierkloof lower	33°39'S 24°31'E	240	40	Closed/open gorge, riverine/slopes, south
22	Baviaanskloof	Grootrivierpoort	33°43'S 24°38'E	140	10	Open gorge, riverine/slopes, west
23	Groendal	Zungarivier (Chase's kloof)	33°41'S 25°14'E	150	150	Open valley, alluvial/slopes, west

TABLE 2.—Number of species by growth forms for the forest sites on the inland mountains of the southern Cape

Site no.	Mountain range and study area	Number of species					Total
		Trees & shrubs	Lianes & vines	Ferns	Geophytes & graminoids	Forbs & soft shrubs	
	Rooiberg (mean spp/site)	27.7	6.0	10.3	4.3	5.7	54.0
1.	Bosrivier upper	21	4	12	3	3	43
2.	Bosrivier lower	30	6	7	5	6	54
3.	Assegaibosrivier	32	8	12	5	8	65
	Kamanassie (mean spp/site)	18.5	5.5	11.5	5.0	8.0	48.5
4.	Kluesrivier	24	7	15	5	13	64
5.	Meulrivier upper	13	4	8	5	3	33
	Swartberg (mean spp/site)	15.1	3.0	6.9	2.1	3.3	30.4
6.	Waterkloof	13	5	12	5	7	42
7.	Seweweekspoort	16	3	4	0	3	26
8.	Swartbergpoort	15	4	7	2	4	32
9.	Swartberg Pass	10	1	13	4	1	29
10.	Rust-en-Vrede	18	4	10	3	6	41
11.	Huisrivier upper	11	1	5	1	2	20
12.	Meiringspoort	21	4	2	2	2	31
13.	Tierkloof	14	1	4	1	2	22
14.	Cheridouwspoort	18	4	5	1	3	31
	Kouga-Baviaanskloof (mean spp/site)	35.4	7.0	9.0	5.3	5.3	62.0
15.	Sapreerivier	35	7	12	3	4	61
16.	Doringkloof	42	10	10	2	8	72
17.	Diepnekkloof (Bosrug)	31	5	7	5	6	54
18.	Geelhoutbos	27	6	6	7	1	47
19.	Assegaaikloof	35	7	4	4	5	55
20.	Witrivierkloof upper	8	1	10	3	2	24
21.	Witrivierkloof lower	53	7	16	10	10	96
22.	Grootrivierpoort	52	13	7	8	6	86
	Groendal						
23.	Zungarivier (Chase's kloof)	76	15	12	12	12	127
	Mean spp/site	26.7	5.5	8.7	4.2	5.1	50.2
	Total	118	29	38	22	43	250

The relationship between the number of woody species (plus vines) or the number of herbaceous species in a forest and the altitude, forest area and direct distance (km) to the nearest source area was determined by means of stepwise multiple regression (STSC 1986). Log transformations were used for all variables because of the highly skew nature of the observations, a procedure usually followed in such studies (Bond *et al.* 1988). The southern Cape forests (Geldenhuys 1993a), marked in black as 'indigenous forest', and 'island' coastal forest west of Port Elizabeth (Figure 1) were considered to be the nearest source areas.

The distribution of taxa, mainly woody species, on the inland mountains was represented by means of tables which indicate the frequency of species on each particular mountain range or in similar sites within a range. The sites were grouped on the basis of assumed dispersal barriers and corridors, as follows: Swartberg sites in three subgroups, i.e. on the northern slopes, at high altitudes and on the southern slopes; Rooiberg; Kamanassie; Kouga-Baviaanskloof; Grootrivierpoort, including the lower site of the Witrivierkloof; and the Groendal site (see Tables 5–8). The most likely dispersal mechanisms for the species are indicated and are based on Coates Palgrave (1977) and my own observations (Geldenhuys 1993a).

The plant nomenclature follows Arnold & De Wet (1993) and the plant author names are according to Brummitt & Powell (1992).

4 RESULTS

4.1 Species richness

The species are listed in the Appendix and summarized by growth forms for the different sites (Table 2). Woody plants and vines form the bulk of the species.

Species numbers vary greatly between sites. In general there is a decline in species richness from east to west and from south to north. The mean number of species per site in the Kouga-Baviaanskloof complex is double the number in the Swartberg range. Note however that the mean number of species, particularly woody species, in the Rooiberg forests tends to be higher than the number in the Kamanassie forests.

4.2 Relationship between species richness and altitude, forest area and distance from source

The number of woody species (plus vines) is significantly correlated with altitude and forest area (Table 3), but not with distance to source area. Altitude alone ex-

TABLE 3.—Analysis of variance for the stepwise multiple regression of the dependence of the (log) number of woody species and vines in a forest on its altitude and area

Independent variable	Coefficient	Standard error	t-value	Significance level
Constant	3.132426	0.221281	14.1559	0.0000
Log Altitude, m	-0.635723	0.078427	-8.1059	0.0000
Log Area, ha	0.195371	0.043653	4.4756	0.0002

R² (adjusted for Df) = 0.8582; standard error of the estimate = 0.09751.

plains 74% of the variation in number of woody species. The number of herbaceous species is significantly correlated only with forest size, but this regression model explains only 18% of the observed variation.

4.3 Distribution of taxa on different mountain complexes

Only 10% of the species occur in more than 50% of the sites and these are mostly tree and shrub species (Table 4). For example, 48 of the 118 tree and shrub species occurred in one or two sites only, i.e. 10% or less of the sites. The pattern of occurrence of species on the different mountain ranges became clearer when the pattern was considered in relation to the distribution range of species in both the inland and coastal forests.

4.3.1 Widespread species on the inland mountains

Species which occur in more than 50% of the sites occur in most sites of all the mountain groups (Table 5). Site preferences of the species are based on their occurrence in the coastal forests (Geldenhuys 1993a). The Kamanassie sites lack several species which have a preference for drier habitats although these species occur in the high altitude sites of the Swartberg. Those which do occur in the Kamanassie are confined to the lower end of Kluesrivier.

4.3.2 Species widespread in coastal forests but with limited spread in study area

Very few of the widespread species of the coastal forests which have a limited spread on the inland mountains do occur in the Swartberg range (Table 6). Those which do occur there are confined to the southern sites. Note again that very few of these species occur in the Kamanas-

sie. However, two of the Kamanassie species are absent from the Rooiberg, i.e. *Rapanea melanophloeos* and *Diospyros whyteana*. *Ocotea bullata* is confined to the Kamanassie and one site in the Rooiberg. Many of the Rooiberg species are absent from the Kamanassie. The majority of the species occur in Groendal and Grootrivierpoort and in one or more sites of the Kouga-Baviaanskloof, and many of these are absent from the Kamanassie or Rooiberg. Note the decrease in number of species from Groendal through Grootrivierpoort to the Baviaanskloof.

4.3.3 Species with limited/disjunct distribution in, or absent from, the coastal forests

These species fall in two groups: those which are confined to the western ranges, i.e. Swartberg, Rooiberg and Kamanassie; and those which are confined to the eastern ranges (Table 7). Note again the decrease in number of species from Groendal through Grootrivierpoort to the Baviaanskloof.

4.3.4 Endemic species of the region

Nine woody species are endemic to the study area, or have their main distribution in the southern Cape. Of these only *Virgilia divaricata* is widespread in the study area (Table 8). *Laurophyllus capensis*, which has a wide distribution in the coastal areas, is confined to a few sites in the Groendal area where it grows in association with *V. divaricata*. *Strelitzia alba*, not recorded during this study, has since been recorded from one locality in the Kouga Mountains (M. Yates pers. comm. 1991; see Geldenhuys 1992a for its distribution in the coastal forests).

TABLE 4.—Absolute and relative frequencies by which species of different growth forms occur in the 23 forested study sites in the inland mountains of the southern Cape

Frequency of occurrence		Number of species				
Absolute number of sites	Relative % of all sites	Trees & shrubs	Climbers	Ferns	Herbs	
					Monocots	Dicots
1-2	1-10	48	14	16	6	28
3-4	11-20	20	6	7	9	9
5-7	21-30	24	4	4	4	3
8-9	31-40	9	1	4	1	1
10-11	41-50	2	1	3	1	1
12-13	51-60	4	-	-	-	1
14-16	61-70	6	2	2	1	-
17-18	71-80	1	1	2	-	-
19-20	81-90	4	-	-	-	-
Total number of species		118	29	38	22	43

TABLE 5.—Distribution and fruit/seed dispersal of species widespread in forested sites on the inland mountain ranges of the southern Cape

Species ¹	Mountain range ²							
	SB ³			RB	KN	BK	GR	GD
	N	U	S					
	Number of sites ⁴							
	3	2	4	3	2	6	2	1
Moist sites								
• <i>Ilex mitis</i>	2	2	4	3	2	4	1	1
• <i>Halleria lucida</i>	3	2	3	3	2	4	1	1
• <i>Kiggelaria africana</i>	2	2	3	2	2	5	2	1
• <i>Maytenus acuminata</i>	3	1	2	3	2	6	1	1
+ <i>Cunonia capensis</i>	2	1	3	3	2	4	1	1
• <i>Myrsine africana</i>	3	2	3	2	1	1	1	-
• <i>Pterocelastrus tricuspidatus</i>	1	-	1	3	2	5	2	1
# <i>Secamone alpini</i>	1	-	2	3	2	4	2	1
• <i>Zantedeschia aethiopica</i>	3	2	2	3	-	3	1	-
# <i>Blechnum australe</i>	2	2	4	2	2	4	1	1
# <i>Blechnum capense</i>	2	1	3	2	2	3	1	1
# <i>Blechnum punctulatum</i>	3	-	4	3	2	4	2	-
# <i>Todea barbara</i>	1	1	3	2	2	4	1	1
Dry sites								
• <i>Olea europaea</i> subsp. <i>africana</i>	2	1	4	3	-	4	2	1
• <i>Maytenus heterophylla</i>	1	1	3	2	-	5	2	1
• <i>Cussonia spicata</i>	2	-	4	3	-	3	1	1
+ <i>Buddleja salviifolia</i>	3	1	3	1	-	3	-	1
• <i>Rhus rehmanniana</i>	2	2	1	2	2	5	-	1
• <i>Rhus lucida</i>	3	1	3	3	1	1	-	-
+ <i>Dipogon lignosus</i>	2	1	2	3	1	6	1	1
• <i>Colpoön compressum</i>	2	-	4	2	1	2	2	1
• <i>Diospyros dichrophylla</i>	-	-	3	3	1	3	2	1
• <i>Asparagus aethiopicus</i>	2	-	4	3	1	3	-	1
+ <i>Pelargonium zonale</i>	2	-	4	3	1	3	-	-

¹ Fruit/seed dispersal mechanisms: •, bird/mammal; +, small/large dry seed not dispersed by wind; #, wind dispersal.
² Mountain range: SB, Swartberg (see ³ below); RB, Rooiberg (sites 1–3); KN, Kamanassie (sites 4, 5); BK, Baviaanskloof (sites 15–20); GR, Grootrivier (sites 21, 22); GD, Groendal (site 23).
³ N, north (sites 8, 13 & 14); U, upper (sites 9 & 11); S, south (sites 6, 7, 10 & 12).
⁴ Maximum number of sites per range for comparison with number of sites in which a species is present.

4.4 Seed dispersal mechanisms

The majority of woody species (Tables 5–8) have fleshy fruits or seeds which are dispersed by frugivorous birds and/or mammals. Among the plants with dry propagules, only the ferns, the liane *Secamone alpini* and the two *Brachylaena* species are readily dispersed by wind. *Cunonia capensis*, *Nuxia floribunda*, *Buddleja saligna* and *B. salviifolia* produce small seeds in capsules which may be blown over short distances in strong wind. *Gonioma kamassi*, *Ptaeroxylon obliquum* and some of the other species have winged seeds which are not well suited for wind dispersal. Note that the majority of endemic species (Table 8) have dry seeds which are not particularly adapted for dispersal over longer distances.

5 DISCUSSION

5.1 Species richness

The forests on the inland mountains of the southern Cape contain 118 tree and woody shrub species, 24 of which are not included in the 140 tree and shrub species of the coastal forests (Geldenhuys 1993a). The difference in number of species of the herbaceous growth forms be-

tween the two areas is much larger. It has been assumed that woody species are more persistent in suitable habitats because the majority of them can resprout after fire, and that they create the micro-habitat for forest understorey plants. In this discussion interpretation of the patterns in species richness and composition is almost confined to the woody species.

5.2 Habitat preferences of species

Habitat preferences of species along an altitudinal gradient do not explain the major differences in species composition of forests in different parts of the inland mountains. The decrease in species richness of woody plants and vines with increasing altitude suggests that many species cannot grow at high altitude. The majority of the widespread species of the coastal forests which have a limited distribution in the inland sites are indeed confined to the low-lying mountain valleys and riverine sites. However, these species are also absent from similar sites on the northern side of the Swartberg range, and many are absent from similar sites on the southern Swartberg, the Kamanassie and the Rooiberg (Table 6).

TABLE 6.—Distribution and fruit/seed dispersal of species widespread in the coastal forests of the southern Cape but with a limited spread in the study area

Species ¹	Mountain range ²							
	SB ³			RB	KN	BK	GR	GD
	N	U	S					
	Number of sites ⁴							
	3	2	4	3	2	6	2	1
• <i>Ocotea bullata</i>	-	-	-	1	2	-	-	-
• <i>Olinia ventosa</i>	-	-	-	3	2	3	2	1
• <i>Cassine peragua</i>	-	-	-	3	2	2	2	1
• <i>Rapanea melanophloeos</i>	-	-	1	-	2	2	2	1
• <i>Diospyros whyteana</i>	-	-	-	-	2	1	2	1
• <i>Carissa bispinosa</i>	-	-	-	3	-	3	2	1
+ <i>Nuxia floribunda</i>	-	-	-	3	-	4	2	1
• <i>Curtisia dentata</i>	-	-	-	3	-	1	2	1
• <i>Allophylus decipiens</i>	-	-	-	2	-	4	2	1
• <i>Scutia myrtina</i>	-	-	-	3	-	-	1	1
• <i>Grewia occidentalis</i>	-	-	-	2	-	4	2	1
+ <i>Buddleja saligna</i>	-	-	1	2	-	2	1	1
• <i>Canthium inerme</i>	-	-	-	2	-	1	2	1
• <i>Olea capensis</i> subsp. <i>capensis</i>	-	-	-	1	-	1	2	-
• <i>Sideroxylon inerme</i>	-	-	-	1	-	3	2	1
• <i>Pittosporum viridiflorum</i>	-	-	-	-	-	5	2	1
• <i>Ficus burtt-davyi</i>	-	-	2	-	-	5	2	1
• <i>Celtis africana</i>	-	-	-	-	-	4	2	1
• <i>Ficus sur</i>	-	-	-	-	-	4	2	1
+ <i>Gonioma kamassi</i>	-	-	-	-	-	3	2	1
• <i>Podocarpus falcatus</i>	-	-	-	-	-	1	2	1
• <i>Apodytes dimidiata</i>	-	-	-	-	-	1	2	1
• <i>Vepris lanceolata</i>	-	-	-	-	-	2	1	1
• <i>Dovyalis rhamnoides</i>	-	-	-	-	-	1	1	1
• <i>Clausena anisata</i>	-	-	-	-	-	1	1	1
• <i>Ekebergia capensis</i>	-	-	-	-	-	1	1	1
• <i>Capparis sepiaria</i>	-	-	-	-	-	1	2	1
• <i>Cassine aethiopica</i>	-	-	-	-	-	1	2	1
• <i>Canthium mundianum</i>	-	-	-	-	-	1	1	-
• <i>Putterlickia pyracantha</i>	-	-	-	-	-	4	2	-
+ <i>Calodendrum capense</i>	-	-	-	-	-	-	1	1
• <i>Podocarpus latifolius</i>	-	-	-	-	-	-	1	1
• <i>Rothmannia capensis</i>	-	-	-	-	-	-	1	1
• <i>Psyrax obovata</i> & others ⁵	-	-	-	-	-	-	1	1
• <i>Ochna arborea</i>	-	-	-	-	-	-	-	1
• <i>Olea capensis</i> subsp. <i>macrocarpa</i>	-	-	-	-	-	-	-	1
• <i>Cassine papillosa</i> & others ⁶	-	-	-	-	-	-	-	1

¹ Fruit/seed dispersal mechanisms: •, bird/mammal; +, small/large dry seed not dispersed by wind.
² Mountain range: SB, Swartberg (see ³ below); RB, Rooiberg (sites 1–3); KN, Kamanassie (sites 4, 5); BK, Baviaanskloof (sites 15–20); GR, Grootrivier (sites 21, 22); GD, Groendal (site 23).
³ N, north (sites 8, 13 & 14); U, upper (sites 9 & 11); S, south (sites 6,7, 10 & 12).
⁴ Maximum number of sites per range for comparison with number of sites in which a species is present.
⁵ Species which occur in only the GR & GD sites.
⁶ Species which occur only in Groendal.

Where habitat preferences have been attached to some species (Table 5), their demonstrated wide tolerances do not explain their absence from certain forests. The widespread species associated with moist coastal sites, occur on the inland sites both at high and low altitudes and in sites which are relatively dry. In several sites they are not confined to the moist, cool sites along the streams, but grow on steep, exposed slopes and often shallow, rocky sites far above the streams, for example in the Kamanassie, the upper Bosrivier, Meiringspoort and Sappreerivier

sites. Only widespread inland species which are associated with both dry and moist coastal sites, grow in the northern Swartberg sites (Table 5), often where the stream courses open up to the north into the arid Great Karoo.

5.3 Species-area relationships and long-distance dispersal

Area is a significant variable in the regression models; this explains the richness of both woody and herbaceous species but in both cases accounts for a relatively small

TABLE 7.—Distribution and fruit/seed dispersal of species which have a limited or disjunct distribution in, or which are absent from the coastal forests of the southern Cape

Species ¹	Mountain range ²							
	SB ³			RB	KN	BK	GR	GD
	N	U	S					
	Number of sites ⁴							
	3	2	4	3	2	6	2	1
Species of coastal forest								
• <i>Pterocelastrus rostratus</i>	-	1	2	2	-	-	-	-
• <i>Diospyros glabra</i>	1	-	2	-	-	-	-	-
# <i>Brachylaena neriifolia</i>	1	1	3	2	2	-	-	-
• <i>Hippobromus pauciflorus</i>	-	-	-	-	-	2	2	1
+ <i>Schotia latifolia</i>	-	-	-	-	-	4	2	1
# <i>Brachylaena glabra</i>	-	-	-	-	-	2	1	1
+ <i>Plumbago auriculata</i>	-	-	-	-	-	2	2	1
• <i>Ochna serrulata</i>	-	-	-	-	-	-	2	1
• <i>Canthium ciliatum</i>	-	-	-	-	-	-	1	1
• <i>Canthium pauciflorum</i>	-	-	-	-	-	-	-	1
• <i>Strychnos decussata</i>	-	-	-	-	-	-	-	1
+ <i>Trichocladus ellipticus</i>	-	-	-	-	-	-	-	1
Species outside coastal forest								
• <i>Diospyros scabrida</i>	-	-	-	-	-	4	1	1
• <i>Pavetta lanceolata</i>	-	-	-	-	-	-	1	1
• <i>Teclea natalensis</i>	-	-	-	-	-	-	2	-
+ <i>Ptaeroxylon obliquum</i>	-	-	-	-	-	-	-	1
• <i>Pleurostyliia capensis</i>	-	-	-	-	-	-	-	1
• <i>Eugenia zeyheri</i>	-	-	-	-	-	-	-	1
• <i>Chaetacme aristata</i>	-	-	-	-	-	-	-	1

¹ Fruit/seed dispersal mechanisms: •, bird/mammal; +, small/large dry seed not dispersed by wind; #, wind dispersal.
² Mountain range: SB, Swartberg (see ³ below); RB, Rooiberg (sites 1–3); KN, Kamanassie (sites 4, 5); BK, Baviaanskloof (sites 15–20); GR, Grootrivier (sites 21, 22); GD, Groendal (site 23).
³ N, north (sites 8, 13 & 14); U, upper (sites 9 & 11); S, south (sites 6, 7, 10 & 12).
⁴ Maximum number of sites per range for comparison with number of sites in which a species is present.

TABLE 8.—Distribution and fruit/seed dispersal in the study area of endemic species of the region

Species ¹	Mountain range ²							
	SB ³			RB	KN	BK	GR	GD
	N	U	S					
	Number of sites ⁴							
	3	2	4	3	2	6	2	1
+ <i>Lachnostylis bilocularis</i>	-	-	1	2	-	-	-	-
+ <i>Virgilia divaricata</i>	-	-	1	-	2	2	1	1
+ <i>Calpurnia villosa</i>	-	-	1	-	-	-	1	-
+ <i>Widdringtonia schwarzii</i>	-	-	-	-	-	2	-	-
• <i>Smelophyllum capense</i>	-	-	-	-	-	4	2	1
+ <i>Loxostylis alata</i>	-	-	-	-	-	1	2	1
+ <i>Atalaya capensis</i>	-	-	-	-	-	-	1	-
+ <i>Sterculia alexandri</i>	-	-	-	-	-	-	-	1
+ <i>Laurophyllus capensis</i>	-	-	-	-	-	-	-	1

¹ Fruit/seed dispersal mechanisms: •, bird/mammal; +, small/large dry seed not dispersed by wind.
² Mountain range: SB, Swartberg (see ³ below); RB, Rooiberg (sites 1–3); KN, Kamanassie (sites 4, 5); BK, Baviaanskloof (sites 15–20); GR, Grootrivier (sites 21, 22); GD, Groendal (site 23).
³ N, north (sites 8, 13 & 14); U, upper (sites 9 & 11); S, south (sites 6, 7, 10 & 12).
⁴ Maximum number of sites per range for comparison with number of sites in which a species is present.

portion of the variation. Direct distance from the source areas ranges from 30 to 80 km but is an insignificant variable in the regression models. For example, the Kamanassie Forests are some of the largest in the study area, are the closest to the coastal forests, particularly the large forests north of Knysna, and represent the moistest sites; yet they contain fewer species than the Rooiberg Forests and lack several species which are present in the Rooiberg. The Rooiberg is a drier mountain, has small forests and its closest source areas are scattered forests between Mossel Bay and George to the southeast and some Langeberg forests west of Riversdale.

The distribution patterns of very few species support claims of long-distance dispersal despite the fact that the majority of tree and shrub species have fleshy fruits or seeds, many of which I have observed being eaten by birds in the coastal forests.

- *Rapanea melanophloeos* and *Ficus burtt-davyi* occur in one and two sites respectively in the Swartberg range which could be attributed to long-distance dispersal. *Ocotea bullata* may have been dispersed into the Rooiberg and Kamanassie from relatively nearby forests with *O. bullata* which exist on the northern slopes of the Langeberg (Garcia Pass near Riversdale) and Outeniqua Mountains (Robinson Pass near Mossel Bay and near Noll west of Uniondale).

- Most of the species which are present in the Rooiberg but absent from the Kamanassie are generally readily dispersed by birds. Their absence from the Kamanassie and the limited distribution in the study area of other similarly readily dispersed species of the coastal forests such as *Apodytes dimidiata*, the two *Podocarpus* species, the two *Olea capensis* subspecies, *Psydrax obovata* and *Canthium mundianum* casts doubt on the relevance of long-distance dispersal in the study area.

- Several species which release minute dry seeds from dry capsules, but which are not effectively dispersed by wind, show distribution patterns which are similar to the patterns of frugivorous species. Examples are *Cunonia capensis*, *Nuxia floribunda*, *Buddleja saligna* and *B. salviifolia*. Their dispersal by birds or mammals is very unlikely.

- The absence of suitable dispersal vectors may be the reason for the insignificance of long-distance dispersal. The sites were visited during different seasons over several years but only one Rameron pigeon (*Columba arquatrix*) was seen in the Swartberg Pass Forest. No studies exist to indicate the migration patterns of frugivorous birds in the southern Cape. It has been suggested that the Rameron pigeon migrates up and down the coast (Phillips 1927). That Rameron pigeons would fly from the coast where food sources are more readily available to the inland mountain forests where their food sources are more limited and possibly irregularly available seems highly unlikely. Small flocks of Red-winged starlings (*Onychognathus morio*) were often seen in the vicinity of the inland forests, but rarely seen along the coast.

5.4 Dispersal barriers and corridors

The parallel mountain ranges are obvious barriers to the dispersal of forest taxa from the coast to the inland forests. The mountain ridges experience strong, cold winds and extreme temperatures. Ice often forms in the sheltered gullies near the top (pers. obs.). Frequent controlled and natural fires

in the fynbos on the mountain slopes prevent the establishment of forest species in the exposed sites and confine or eliminate existing forests. This was observed in most of the sites or was evident in the small sizes of trees near the forest edge in more protected sites.

Dry lowlands and valleys of the Little Karoo minimize the number of species which are able to cross them by means of establishment in small bush clumps in a stepping-stone fashion.

The obvious dispersal corridors are the Zunga River, the Gamtoos River through the Grootrivierpoort and Baviaanskloof, the Keurbooms River and the Gouritzpoort. The first two river systems are effective corridors for stepping-stone dispersal. The sites along the Zunga River the end constitute of the subtropical transitional thicket and riverine forests which are connected with the Alexandria and other coastal forests. Many streams run into the Baviaanskloof River from the mountain ridges to its north and south and provide refuge sites for forest species. The Baviaanskloof shares many of the species which occur in the Grootrivierpoort and Witrivierkloof and at Groendal. The remaining two rivers are not effective corridors. The Keurbooms River does not breach the relatively low Outeniqua-Tsitsikamma mountain ridge to provide direct and easy access for dispersal of forest species from the large Knysna forests to the Kamanassie Mountains. The Gouritzpoort contains no sheltered sites for forest establishment and north of the poort is an arid lowland. It is not connected with any nearby forests to the south of the poort. It may have been an effective dispersal corridor in earlier, moister periods, but not under the present climate.

5.5 Forest migration in relation to climatic change

Following on from the earlier discussion, it is therefore suggested that the variation in species richness on the inland mountains is mainly the result of different degrees of intermingling during the contraction and expansion of the different floras due to climatic and landscape changes since the Palaeocene. Only tree and woody shrub species have been considered for this interpretation because it has been assumed they are the key elements which create the specific micro-habitats for herbaceous elements of the understorey of particular vegetation units. Certain understorey species should therefore correlate with the distribution pattern of particular groups of tree species. Factors such as the altitudinal gradient, forest size, site preferences and dispersal corridors and mechanisms are merely contributing to this variation within a particular mountain range. In this study at least four floras can be recognized from the distribution patterns of the species as listed in Tables 5 to 8, namely: temperate or austral forest relicts; subtropical forest; subtropical transitional thicket and karroid riverine woodland.

5.5.1 Temperate forest

It is suggested that most of the widespread inland species characteristic of moist sites (Table 5) represent relicts of the temperate austral forests (such as *Cunonia capensis*) or high-altitude forests of tropical latitudes (such as *Ilex mittis*, *Halleria lucida* and *Kiggelaria africana*) which cov-

ered the southern tip of Africa during the Palaeocene, rather than recent dispersal events. These temperate forests were eliminated with changes toward warmer and more humid climates associated with the northward drift of the African continent (Axelrod & Raven 1978; Deacon 1983). These constituent species grow in forests on all the mountain complexes in the study area, and are the only species which grow in sheltered sites on the northern slopes of the Swartberg range. They are also the main species of the forests in the cool, sheltered kloofs and gorges of the inland mountain ranges in the southwestern Cape (pers. obs.). Many of them occur in the isolated Afromontane forests of southern and eastern Africa (Killick 1963; Chapman & White 1970; Dowsett-Lemaire 1988). The poorts through the Swartberg range had breached the ranges by the early Tertiary (Lenz 1957) and would have allowed dispersal of other readily dispersed species through the poorts from south to north, if they were present by that time. Even if it is argued that in more recent times the fleshy-fruited tree species may have been dispersed to the northern side of the Swartberg by birds, the argument does not account for the presence of *Canonia capensis* with its small, dry seeds. The wide habitat tolerances of these species enabled them to survive and to occur widespread in the study area, and in southern Africa (Geldenhuis 1992b).

Species which could be added to the list of temperate forest species are *Pterocelastrus rostratus*, *Diospyros glabra* and *Brachylaena neriifolia*. Their eastern distribution limits in the study area (Table 7) coincide with the longitude of their eastern limits in the coastal forests (Geldenhuis 1992a). Their distribution patterns suggest a more continuous distribution at some early period which was later fragmented into their present pattern.

5.5.2 Subtropical forest

It is suggested that the widespread coastal forest species with limited spread in the inland sites (Table 6) represent elements of the subtropical forest which replaced the temperate forests since the Oligocene-Miocene (Axelrod & Raven 1978; Deacon 1983). Most of these species occur also in the coastal forests of the southern and southwestern Cape (Geldenhuis 1993a; McKenzie 1978). These forests have expanded from the east. The easterly orientation of the Zunga and Gamtoos Rivers and the Kouga-Baviaanskloof valleys suggests that they would have been more readily colonized by the expanding subtropical forests. The Gouritz River breached the Langeberg-Outeniqua range during the late Cretaceous as a subsequent poort, i.e. it developed along a relatively weaker part of the range by a headward eroding stream (Lenz 1957). With widespread forest along the coast south of the Outeniqua-Langeberg Mountains and with a more humid climate (Hendey 1983) the Gouritz River could have been a suitable dispersal corridor for some species to enter the southern sides of the Rooiberg. The Rooiberg-Gamka mountain range forms a loose connection to the southeast with the Outeniqua range and may have had sheltered sites on the southwestern side. Today several species of the western fynbos element, e.g. *Minetes cucullatus*, that are characteristic of the wetter coastal ranges, also occur on the Rooiberg-Gamka range and the adjacent Outeniqua range (Taylor 1979; J.H.J. Vlok pers. comm. 1988). They support the dispersal route suggested

for the forest species, although the fynbos migration relates to Late Pleistocene times and different environmental conditions which would not support forest.

The nature of the deposits in the Oudtshoorn Basin suggests that the climate during the Late Cretaceous was similar to the present semi-arid climate and the Olifants River portion of the breach between Rooiberg and Gamka Hill occurred as late as Plio-Pleistocene (Lenz 1957). This semi-arid climate and the late breach would have prevented the spread of subtropical forest towards the Swartberg. The absence of a direct corridor between the Keurbooms River and the Kamanassie accounts for the absence from the Kamanassie of several Knysna forest species, which are present in the Rooiberg (Table 6).

Some of the widespread as well as disjunctly distributed coastal species are confined to the Groendal, Grootrivierpoort and lower Witrivierkloof sites (Tables 6 & 7; Appendix). Two possible explanations for this pattern are: 1, most of these species have relatively large fruits or seeds which require specialized dispersal vectors. The seeds of some species such as *Podocarpus latifolius* and *Calodendrum capense* lose viability fast when they dry out, and those of other species such as *Olea capensis* subsp. *macrocarpa* and *Cassine papillosa* have long germination periods due to woody seed coats (Geldenhuis 1975, 1996) and are then liable to predation by rodents (pers. obs.). However, others with similar seed types occur further into the Kouga-Baviaanskloof complex such as *Ekebergia capensis* and *Podocarpus falcatus* (both are dispersed by bats; see Geldenhuis 1993b for *P. falcatus*); 2, a more likely explanation is that the subtropical forests expanded in different waves and that each wave contained a different set of species. The expansion and contraction could be related to successive periods of high and low sea levels respectively, which in turn were associated with humid and arid periods respectively (Hendey 1983). During later periods of forest expansion along the coast, some areas, particularly the more arid inland areas, may not have been suitable for the colonization by forest species.

For example, *Podocarpus falcatus* occurs as far west as Swellendam, and *P. latifolius* as far west as the Cape Peninsula (Von Breitenbach 1986). Both grow in small forest patches near the southern exit of the Gouritz River through the Langeberg-Outeniqua ranges. Both are readily dispersed in the southern Cape coastal forests (Geldenhuis 1980, 1993a, b) but have a limited entry in the Baviaanskloof and are absent from the Rooiberg and Kamanassie. It is suggested that they represent a relatively late southwestern expansion of the subtropical forests when barriers of semi-arid lowlands inland of the coastal mountains prevented their spread inland. This implies that the two *Podocarpus* species have a tropical origin and are not part of the austral flora as has often been suggested (e.g. Levyns 1964). Their large fruit size indicates a tropical affinity (Givnish 1980), in contrast to the small fruit size of austral podocarps of Australia, New Zealand and Chili (pers. obs.). It is suggested that the fossil podocarp pollens from some southwestern Cape sites (e.g. Coetzee 1986) may represent austral podocarps which became extinct with the regression of the early temperate forests and before the present species arrived in the area.

Some species represent the spread of subtropical transitional thicket (Cowling 1984; Everard 1987). Species

such as *Ptaeroxylon obliquum*, *Diospyros scabrida* and *Pavetta lanceolata* have not yet reached the southern Cape coastal forests. Others have reached the southern Cape but were cut off by the Late Pleistocene-Holocene marine transgression, e.g. *Hippobromus pauciflorus*, *Schotia latifolia* and *Plumbago auriculata* (Geldenhuis 1992a).

Some coastal dune forest species, such as *Strychnos decussata* and *Eugenia zeyheri*, require specialized sites which prevented their spread inland. For example, *S. decussata* grows on a terrace along the Zunga River in a site similar to that in which the species grows in Nature's Valley along the southern Cape coast (Geldenhuis 1986). *Strelitzia alba* also falls in this category.

Some species, such as *Trichocladus ellipticus*, represent relicts of a retreating forest flora (Geldenhuis 1992a).

5.5.3 Subtropical transitional thicket and karroid woodland

The widespread inland species of drier sites (Table 5) are generally associated with subtropical transitional thicket (Cowling 1984; Everard 1987). They have probably become mixed with the more tolerant moist forest elements with the increasing aridity since the beginning of the Miocene-Pliocene (Deacon 1983). They occur in few of the sites at higher altitudes. They are more prominent in the bush clumps and subtropical transitional thicket of the more arid lowlands and riverine sites in the drier, open valleys of the Baviaanskloof and Karoo. They occur in the drier parts of moist sites as they are found where streams from the mountains open up into the dry valleys, or on the drier slopes above the streams, or along open valleys or gorges such as Meiringspoort. Seeds of several of the species were found along the krantzies above the study sites and it is assumed that Red-winged starlings (*O. morio*) dispersed the seeds from the lowlands or other nearby sites. Many of these species are, however, absent from the Kamanassie sites although they are present in the lowlands further away from the mountain. The higher (Eo-Oligocene) and lower (Mio-Pliocene) surfaces on the southern side of the Kamanassie (Lenz 1957) could account for this absence. At Boomplaas Cave, between the Swartberg Pass and Rust-en-Vrede sites, charcoal assemblages indicate that *A. karroo* only became dominant in the late Holocene during more mesic conditions (Scholtz 1986). This species was absent from charcoal layers older than 12 000 years although it was apparently a much preferred firewood. It became a major component of woodland in the valley near the cave after 5 000 yBP, after an initial spread into the valley during the early Holocene (Deacon *et al.* 1983).

5.6 Endemic species

The endemic species represent two major groups: forest margin species such as *Virgilia divaricata* (Phillips 1926), *Laurophyllum capensis* (Phillips 1931; Geldenhuis 1993a) and *Widdringtonia schwarzii* (Lückhoff 1963); and species of drier sites such as *Lachnostylis bilocularis* and *Loxostylis alata* (Palmer & Pitman 1972). The sites in which the forest margin species mature suggest that they can only persist with less frequent fires than under which fynbos persists. This has been shown for *L. capensis* (Vlok & De Ronde 1989). Trees of *V. divaricata* (Phillips 1926) and *Widdringtonia schwarzii* (Lückhoff 1963) are killed by

fires and depend on reseedling for regeneration. All except *Smelophyllum capense* have dry seeds which do not appear to be readily dispersed. It is assumed that these species have evolved in this region. It is suspected that they formed part of specific vegetation units but became separated and isolated to a lesser or greater degree as a result of their poor dispersability and sensitivity to frequent fires.

The distribution of *Virgilia* (Van Wyk 1986) corresponds with the distribution pattern of the subtropical forest species which expanded during the Oligocene-Miocene. It is suggested that *V. divaricata* was the parent species from which the other species evolved because of its presence in both the inland and coastal forests. Its absence from Rooiberg but presence in Kamanassie suggests that the species became established at a relatively late stage of expansion of subtropical forest. Its crossing of the gap north of the Keurbooms River towards the Kamanassie can perhaps be explained by dispersal of the resistant seeds by primates, particularly the baboon (*Papio ursinus*) and Vervet monkey (*Cercopithecus aethiops*). Both these primates have been seen in stands of *Acacia karroo* and the alien wattle *A. mearnsii* which have seeds very similar to *V. divaricata*. Seeds of *V. divaricata* have been found in the faeces of the baboon in the coastal mountains. Van Wyk (1986) mentioned two forms of the species: a form of drier localities such as in Seweweekspoort, Baviaanskloof and Groendal; and the form of the coastal forests between Humansdorp and George. In the context of the spread of the species I consider the form of drier localities as the first stage and the form of the coastal forest as the second stage.

Lachnostylis bilocularis was recorded in the Rooiberg and Meiringspoort but it also occurs in various localities between Ladismith and Unionsdale (Palmer & Pitman 1972). In Meiringspoort the tree grows in the southern part of the gorge up to a particularly narrow part of the gorge but does not occur north of it. Its distribution suggests that it was more widespread before. The related *L. hirta* occurs in the coastal forests over a somewhat wider range (Palmer & Pitman 1972). It is suggested that *L. hirta* spanned the Gouritz River valley during less arid periods of the Oligocene-Miocene with a wider distribution in the dry, forested coastal areas. *L. bilocularis* evolved inland as an adaptation to dry, open sites and eventually became limited to the present localities when the lowlands became even drier. Both species have dry seeds in dry capsules and are poorly dispersed. *Calpurnia villosa* has a similar but more restricted distribution than *L. bilocularis*, which also centres on the Gouritz River and its tributaries in the Oudtshoorn basin (Palmer & Pitman 1972). The record of *C. villosa* from Grootrivierpoort could be based on my misidentification in the field of *C. aurea*, a species which has a disjunct distribution along the coast (Geldenhuis 1992a).

6 CONCLUSIONS

The systematic survey of forests in the inland mountain ranges in relation to the geomorphological evolution of dispersal corridors which link them with the coastal forests has provided a means to postulate relative dates for the expansion and contraction of floristic elements of both the inland and coastal forests. However, certain assumptions made in this study require to be verified, such as the following:

- Dispersal distances by wind of the small, dry seeds of *Cunonia capensis* and *Nuxia floribunda*.
- Flight patterns of frugivorous birds between the coastal and inland forests, and the feeding behaviour of these birds.
- The phylogenetic relationships of species of genera such as *Lachnostylis* and *Virgilia*, and of provenances of several other species such as *Ilex mitis* and the *Podocarpus* species.

Disturbance regimes in the study area have changed over time. The current man-induced disturbances of the vegetation exert extreme pressures on the forests which persisted in refuge sites in marginal environments. The forest patches should be treated as rare 'species' to allow the natural processes of population migration, settlement and adaptation to continue. The following examples of changed management could provide the required protection to these forests:

- Burning patterns during controlled block burns in catchments which contain forest patches should be reconsidered. The forests should not be used as fire breaks as has been done in several cases. Fires should be burnt down the slopes as would occur with natural fires (Geldenhuys 1994) and not from the bottom of the valleys upwards.
- Smaller alluvial sites along the rivers and the area surrounding the exit of streams from the mountains should not be cultivated, grazed or burnt.

7 ACKNOWLEDGEMENTS

This study formed part of the activities of the Programme for Natural Resources and Rural Development of the Division of Water, Environment and Forestry Technology, CSIR. It was funded by the Department of Water Affairs and Forestry (Forestry Branch). These activities formed part of a Ph.D. study under supervision of Prof. E.J. Moll, formerly of the Department of Botany, University of Cape Town. Several colleagues assisted during the sampling of the forest patches in often very difficult terrain: R. Bartholomew, M.J. Cameron, T. Hoekstra, H.J. Homann, J.H. Koen, H. Kotze, A. Meyer, C.M. van den Berg, C.J. van der Merwe, J.P.L. van der Walt, M. Viviers and J.H.J. Vlok. Mr J. Dobson prepared the map of the study area.

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APPENDIX. SPECIES LIST FOR FORESTS IN INLAND MOUNTAINS OF THE SOUTHERN CAPE

The forest sites are as follows:
Rooiberg: 1, Bosrivier upper; 2, Bosrivier lower; 3, Assegaaibosrivier
Kamanassie: 4, Kluesrivier; 5, Meulrivier upper
Swartberg: 6, Waterkloof; 7, Seweweekspoort; 8, Swartbergpoort (Prins Albert); 9, Swartberg Pass (hotel site); 10, Rust-en-Vrede; 11, Huisrivier upper; 12, Meiringspoort; 13, Tierkloof; 14, Cheridouwspoort
Kouga-Baviaanskloof: 15, Sapreerivier; 16, Doringkloof; 17, Bosrug; 18, Geelhoutbos; 19, Assegaaikloof; 20, Witrivier upper; 21, Witrivier lower; 22, Grootrivierpoort
Groendal: 23, Zungarivier (Chase's kloof)

Species	Forest site																							Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
Canopy and subcanopy tree species																								
<i>Acacia karroo</i> Hayne	-	-	-	-	-	-	•	-	-	-	-	•	-	-	-	•	-	-	•	•	-	•	-	6
<i>Allophylus decipiens</i> (Sond.) Radlk.	•	•	-	-	-	-	-	-	-	-	-	-	-	•	•	•	-	•	-	•	•	-	-	9
<i>Apodytes dimidiata</i> E.Mey. ex Arn.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	•	4
<i>Atalaya capensis</i> R.A.Dyer	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	1
<i>Brachylaena glabra</i> (L.f.) Druce	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	•	•	-	•	4
<i>Buddleja saligna</i> Willd.	•	•	-	-	-	•	-	-	-	-	-	-	-	-	-	•	•	-	-	-	-	•	•	7
<i>Calodendrum capense</i> (L.f.) Thunb.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	2
Canthium																								
<i>ciliatum</i> (Klotzsch) Kuntze	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	2
<i>inerme</i> (L.f.) Kuntze	•	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	•	6
<i>mundianum</i> Cham. & Schlecht.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	•	-	2
<i>pauciflorum</i> (Klotzsch) Kuntze	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
Cassine																								
<i>aethiopica</i> Thunb.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	•	-	3
<i>eucleiformis</i> (Eckl. & Zeyh.) Kuntze	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	1
<i>papillosa</i> (Hochst.) Kuntze	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
<i>peragua</i> L.	•	•	•	•	•	-	-	-	-	-	-	-	-	-	•	•	•	-	-	-	-	•	-	9
<i>Celtis africana</i> Burm.f.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	•	-	•	•	•	7
<i>Chionanthus foveolata</i> (E.Mey.) Stearn	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	2
<i>Clausena anisata</i> (Willd.) Hook.f. ex Benth.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	•	•	3
<i>Cunonia capensis</i> L.	•	•	•	•	•	-	-	-	-	•	•	•	•	•	•	•	•	-	•	-	•	-	•	16
<i>Curtisia dentata</i> (Burm.f.) C.A.Sm.	•	•	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	•	•	7
Cussonia																								
<i>paniculata</i> Eckl. & Zeyh.	-	-	-	-	-	-	-	-	-	-	•	-	•	•	-	•	-	-	-	-	-	-	-	4
<i>spicata</i> Thunb.	•	•	•	-	-	•	•	•	-	•	-	•	-	•	•	•	•	-	-	-	-	•	•	14
Diospyros																								
<i>dichrophylla</i> (Gand.) De Winter	•	•	•	•	-	-	-	-	•	-	•	-	-	•	-	•	-	•	•	-	•	•	•	13
<i>whyteana</i> (Hiern) F.White	-	-	-	•	•	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	•	•	6
<i>Ekebergia capensis</i> Sparrm.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	•	•	3
Euclea																								
<i>racemosa</i> Murray	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	•	-	-	-	-	-	-	-	2
<i>schimperi</i> (A.DC.) Dandy var. <i>schimperi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
<i>undulata</i> Thunb.	-	-	-	•	-	-	-	•	-	•	-	•	-	-	•	-	-	•	-	-	•	-	-	7

Species	Forest site																							Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
<i>Eugenia zeyheri</i> Harv.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
<i>Ficus sur</i> Forssk.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	•	•	•	•	•	7
<i>Gonioma kamassi</i> E.Mey.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	-	•	-	•	•	•	6
<i>Halleria lucida</i> L.	•	•	•	•	•	•	-	•	•	•	•	•	•	•	•	•	•	-	-	•	•	-	-	19
<i>Heteromorpha trifoliata</i> (Wendl.) Eckl. & Zeyh.	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Hippobromus pauciflorus</i> (L.f.) Radlk.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	-	•	•	•	5
<i>Ilex mitis</i> (L.) Radlk.	•	•	•	•	•	•	•	•	•	•	•	•	•	-	•	•	-	•	-	•	•	-	•	19
<i>Kiggelaria africana</i> L.	•	-	•	•	•	•	-	•	•	•	•	•	-	-	•	•	•	•	-	-	•	•	•	19
<i>Loxostylis alata</i> Spreng.f. ex Rchb.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	•	•	4
<i>Maytenus</i>																								
<i>acuminata</i> (L.f.) Loes.	•	•	•	•	•	-	-	•	-	•	•	•	•	•	•	•	•	•	•	•	-	•	•	19
<i>nemorosa</i> (Eckl. & Zeyh.) Marais	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	2
<i>oleoides</i> (Lam.) Loes.	-	•	-	-	-	-	•	•	-	-	-	-	•	•	•	-	-	-	-	-	-	-	-	6
<i>peduncularis</i> (Sond.) Loes.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
<i>undata</i> (Thunb.) Blakelock	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	-	-	-	-	-	-	2
<i>Nuxia floribunda</i> Benth.	•	•	•	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	•	-	•	•	•	10
<i>Ochna arborea</i> Burch. ex DC.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
<i>Ocotea bullata</i> (Burch.) Baill.	•	-	-	•	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
<i>Olea</i>																								
<i>capensis</i> L.																								
subsp. <i>capensis</i>	•	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	•	•	4
subsp. <i>macrocarpa</i> (C.H.Wr.) I.Verd.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
<i>europaea</i> L. subsp. <i>africana</i> (Mill.) P.S.Green	•	•	•	•	•	•	•	•	•	-	-	-	-	•	•	•	•	-	-	-	-	•	•	17
<i>Olinia ventosa</i> (L.) Cufod.	•	•	•	•	•	-	-	-	-	-	-	-	-	-	•	•	•	-	•	•	•	•	•	11
<i>Pappea capensis</i> Eckl. & Zeyh.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	2
<i>Pittosporum viridiflorum</i> Sims	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	•	-	•	•	•	8
<i>Pleurostyliia capensis</i> (Turcz.) Oliv.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
<i>Podocarpus</i>																								
<i>falcatus</i> (Thunb.) R.Br. ex Mirb.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	•	•	•	4
<i>latifolius</i> (Thunb.) R.Br. ex Mirb.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	2
<i>Psydrax obovata</i> (Eckl. & Zeyh.) Bridson	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	2
<i>Ptaeroxylon obliquum</i> (Thunb.) Radlk.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
<i>Pterocelastrus</i>																								
<i>rostratus</i> Walp.	-	•	-	•	-	-	•	-	-	•	•	-	-	-	-	-	-	-	-	-	-	-	-	5
<i>tricuspidatus</i> (Lam.) Sond.	•	•	•	•	•	-	•	•	-	-	-	-	-	-	•	•	•	•	•	-	•	•	•	15
<i>Rapanea melanophloeos</i> (L.) Mez	-	-	-	•	•	-	-	-	-	•	-	-	-	-	•	•	-	-	-	-	-	•	•	8
<i>Rhus</i>																								
<i>chirindensis</i> Baker f.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
<i>lancea</i> L.f.	-	-	•	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	2
<i>lucida</i> L.	•	•	•	•	-	•	•	•	•	•	•	•	•	•	•	-	-	-	-	-	-	-	-	12
<i>Rothmannia capensis</i> Thunb.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	2
<i>Schotia latifolia</i> Jacq.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	•	-	•	•	•	7
<i>Scolopia</i>																								
<i>mundii</i> (Eckl. & Zeyh.) Warb.	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	2
<i>zeyheri</i> (Nees) Harv.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
<i>Sideroxylon inerme</i> L.	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	-	•	-	-	7
<i>Smelophyllum capense</i> (Sond.) Radlk.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	•	-	•	-	•	7
<i>Sterculia alexandri</i> Harv.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
<i>Strychnos decussata</i> (Pappe) Gilg	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Tarchonanthus camphoratus</i> L.	-	•	-	-	-	-	-	-	-	-	-	-	-	•	•	-	-	-	-	-	-	-	•	5
<i>Teclea natalensis</i> (Sond.) Engl.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	-	2
<i>Vepris lanceolata</i> (Lam.) G.Don	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	-	-	-	-	4
<i>Virgilia divaricata</i> Adamson	-	-	-	-	-	•	-	-	-	-	-	-	-	-	•	•	-	-	-	-	•	•	•	7
<i>Widdringtonia schwarzii</i> (Marloth) Mast.	-	-	•	•	-	-	-	-	-	-	-	-	-	-	•	•	-	-	-	-	-	-	-	2
<i>Zanthoxylum capense</i> (Thunb.) Harv.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	1
Shrubs																								
<i>Acokanthera oppositifolia</i> (Lam.) Codd	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	•	•	3
<i>Azima tetraacantha</i> Lam.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	-	-	-	•	•	5
<i>Brachylaena neriifolia</i> (L.) R.Br.	-	-	•	•	•	•	-	-	-	•	•	•	•	•	-	-	-	-	-	-	-	-	-	9
<i>Buddleja</i>																								
<i>salviifolia</i> (L.) Lam.	-	-	•	-	-	-	•	•	•	•	•	•	•	•	•	•	•	-	-	-	-	-	•	12
sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	-	-	-	-	-	-	2
<i>Calpurnia villosa</i> Harv.	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	•	-	2
<i>Capparis sepiaria</i> L. var. <i>citrifolia</i> (Lam.) Toelken	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	•	-	3
<i>Carissa</i>																								
<i>bispinosa</i> (L.) Desf. ex Brenan	•	•	•	-	-	-	-	-	-	-	-	-	-	-	•	•	-	-	•	-	•	•	•	9
<i>haematocarpa</i> (Eckl.) A.DC.	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Cassine</i>																								
<i>parvifolia</i> Sond.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	1
<i>reticulata</i> (Eckl. & Zeyh.) Codd	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	-	•	-	-	-	-	3
<i>tetragona</i> (L.f.) Loes.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	1
<i>Chaetacme aristata</i> Planch.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
<i>Chrysanthemoides monilifera</i> (L.) Norl.	-	-	•	-	•	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
<i>Colpoon compressum</i> P.J.Bergius	-	•	•	•	-	•	•	-	-	•	-	•	•	•	•	•	•	-	-	-	-	•	•	14

Species	Forest site																							Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
<i>Clusia</i>																								
<i>natalensis Bernh.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	1
<i>pulchella L.</i>	-	•	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	-	-	4
<i>Crassula</i>																								
<i>nemerosa (Eckl. & Zeyh.) Endl. ex Walp.</i>	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	2
<i>pellucida L. subsp. marginalis (Dryand. in Aiton) Toelken</i>	-	-	-	•	-	•	-	•	-	•	-	-	-	-	-	•	•	-	-	-	•	•	-	8
<i>Cyrtorchis arcuata (Lindl.) Schltr.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
<i>Didymodoxa caffra (Thunb.) Friis & Wilmot-Deer</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
<i>Euphorbia kraussiana Bernh.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	•	•	3
<i>Galium thunbergianum Eckl. & Zeyh.</i>	-	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Galopina circaeoides Thunb.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	•	-	•	3
<i>Gerbera cordata (Thunb.) Less.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	3
<i>Helichrysum petiolare Hilliard & B.L.Burt</i>	-	-	-	•	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
<i>Hypoestes sp. cf. verticillatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	-	•	•	-	4
<i>Isoglossa proluxa (Nees) Lindau</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	•	2
<i>Jatropha capensis (L.f.) Sond.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	1
<i>Knowltonia vesicatoria (L.f.) Sims subsp. humilis H.Rasm.</i>	•	•	•	-	-	•	-	-	-	•	-	-	-	-	-	-	-	-	-	•	-	-	-	6
<i>Leidesia procumbens (L.) Prain</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	1
<i>Leonotis ocymifolia (Burm.f.) Iwarsson</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	1
<i>Lobelia sp.</i>	-	-	•	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
<i>Nemesia mellissifolia Benth.</i>	-	-	-	•	-	-	-	•	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	3
<i>Oxalis incarnata L.</i>	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	3
<i>Pavonia praemorsa (L.f.) Cav.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	1
<i>Pelargonium</i>																								
<i>ribifolia Jacq.</i>	-	•	•	•	-	•	-	-	-	-	-	-	•	•	•	-	-	-	-	-	-	-	-	7
<i>scabroide Knuth</i>	-	-	-	-	-	-	-	-	-	•	•	•	•	•	-	-	-	-	-	-	-	-	-	5
<i>zonale (L.) L'Hér.</i>	•	•	•	•	-	•	•	•	-	•	-	•	•	•	•	•	•	-	-	-	-	-	-	13
<i>Peperomia</i>																								
<i>retusa (L.f.) A.Dietr.</i>	•	-	•	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	•	-	-	4
<i>tetraphylla (G.Forst.) Hook. & Arn.</i>	-	-	-	•	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
<i>Peucedanum sp.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	1
<i>Plectranthus verticillatus (L.f.) Druce</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	1
<i>Polygala myrtifolia L.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	1
<i>Solanum</i>																								
<i>giganteum Jacq.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	1
<i>retroflexum Dunal</i>	-	-	-	-	-	•	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
<i>tomentosum L.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	1
<i>Sp. cf. Acalypha</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	•	-	2
<i>Stachys</i>																								
<i>aethiopica L.</i>	-	•	•	•	-	-	-	•	•	-	-	-	-	-	•	-	•	-	•	-	•	•	-	10
<i>grandifolia E.Mey. ex Benth.</i>	-	-	-	•	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
<i>Streptocarpus rexii (Hook.) Lindl.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	•	2
<i>Zygophyllum morganiana L.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	1

Cytogenetic studies in some representatives of the subfamily Pooideae (Poaceae) in South Africa. 3. The tribe Poeae

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Keywords: basic chromosome numbers, chromosomes, meiosis, Poaceae, Poeae, polyploidy, Pooideae, South Africa

ABSTRACT

This is a report on chromosome numbers for the tribe Poeae, which is represented in South Africa mainly by naturalized exotics. Chromosome numbers of 67 specimens, representing 26 species and 11 genera, are presented. These numbers include the first reports on *Poa binata* Nees ($n = 3x = 21$ and $n = 4x = 28$), *Puccinellia acroantha* C.A.Sm. & C.E.Hubb. ($n = 3x = 21$) and *P. angusta* (Nees) C.A.Sm. & C.E.Hubb. ($n = x = 7$). New ploidy levels are reported for *Catapodium rigidum* (L.) C.E.Hubb. ($n = 2x = 14$), *Festuca caprina* Nees ($n = 2x = 14$) and *F. scabra* Vahl ($n = x = 7$).

INTRODUCTION

The first paper in this series indicated the importance of determining the ploidy levels and basic chromosome numbers of naturalized and endemic flora in South Africa (Spies *et al.* 1996a). In the second paper chromosome numbers of the rest of the tribe Aveninae were presented (Spies *et al.* 1996b). This third paper in the series on chromosome numbers of representatives of the subfamily Pooideae in South Africa, is restricted to the tribe Poeae.

During this study we followed the classification system of Gibbs Russell *et al.* (1990) for the tribal separation. Therefore we did not recognize the tribe Hainardeae Greuter, and all the species usually belonging to this small tribe are included in the Poeae. The tribe Poeae consists, therefore, of approximately 55 genera and more than 5000 species (Clayton & Renvoize 1986). Most local species belonging to this tribe are naturalized exotics. The Poeae are represented in South Africa by the genera *Briza* L., *Catapodium* Link, *Colpodium* Trin., *Cynosurus* L., *Dactylis* L., *Festuca* L., *Hainardia* Greuter, *Lamarckia* Moench, *Lolium* L., *Parapholis* C.E.Hubb., *Poa* L., *Puccinellia* Parl., *Sphenopus* Trin. and *Vulpia* C.C.Gmel. (Gibbs Russell *et al.* 1990).

The aim of this study is to determine the chromosome numbers, polyploid levels and meiotic chromosome behaviour of the South African representatives of the tribe Poeae. These results will, eventually, be compared with the results obtained from indigenous and endemic taxa to compare the frequency of polyploidy between indigenous and introduced grasses.

MATERIALS AND METHODS

For the purpose of this study, cytogenetic material was collected in two different ways. The material was either collected and fixed in the field, or living material was collected in the field and transplanted in the nurseries of

either the Department of Botany and Genetics, University of the Orange Free State (Bloemfontein) or the National Botanical Institute (Pretoria), where the cytogenetic material was collected and fixed. The specimens used and their localities are listed in Table 1. Voucher specimens are housed either in the Geo Potts Herbarium, Department of Botany and Genetics, University of the Orange Free State, Bloemfontein (BLFU) or in the National Herbarium, Pretoria (PRE).

Anthers were squashed in aceto-carmine and meiotically analysed (Spies *et al.* 1996a). Chromosome numbers are presented as haploid chromosome numbers to conform to previous papers on chromosome numbers in this journal (Spies & Du Plessis 1986a). Genome homology in some tetraploid specimens was determined according to the models described by Kimber & Alonso (1981).

RESULTS AND DISCUSSION

Briza consists of 16 species, with three (*B. maxima* L., *B. minor* L. and *B. subaristatum* Lam.) being naturalized in South Africa. Two of these species were studied. Both were diploid with *B. maxima* having the haploid chromosome number seven ($n = x = 7$) and *B. minor* five ($n = x = 5$) (Table 1). These findings confirm previous reports on chromosome numbers for these species by Fedorov 1969; Ornduff 1967–1969; Moore 1970, 1971, 1972, 1974, 1977; Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991, 1994, who observed tetraploid *Briza* specimens in several species. However, polyploidy seems to be absent in both *B. maxima* and *B. minor* specimens studied here and abroad. Meiosis was regular in both species, and bivalents were formed (Figure 1A & B). These results, in combination with the available chromosome numbers given in the literature consulted, indicate that *Briza* has two basic chromosome numbers, namely five and seven.

Catapodium consists of two species, one of which is naturalized in South Africa [*C. rigidum* (L.) C.E.Hubb.]. Three of the studied specimens were diploid ($n = x = 7$), whereas the other specimen was tetraploid ($n = 2x = 14$) (Table 1). The diploid chromosome number observed sup-

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MS. received: 1996-08-07.

TABLE 1.—Haploid chromosome numbers of representatives of the tribe Poeae (Poaceae, Pooideae) in southern Africa with their voucher specimen numbers and specific localities. Species are listed alphabetically, voucher numbers within a species numerically and the locality is presented according to the system described by Edwards & Leistner (1971)

Taxon	Voucher No.	n	Locality
<i>Briza maxima</i>	<i>Spies 3159</i>	7	WESTERN CAPE.—3218 (Clanwilliam): Versveld Pass, (–DC)
	<i>Spies 3548</i>	7	WESTERN CAPE.—3421 (Riversdale): 4 km from Kweekkraal to Droërivier, (–AA)
	<i>Spies 4420</i>	7	WESTERN CAPE.—3318 (Cape Town): 19 km from Darling to Malmesbury, (–AD)
<i>B. minor</i>	<i>Spies 3239a</i>	5	NORTHERN CAPE.—3229 (Sutherland): 10 km from Sutherland to Matjiesfontein, (–BC)
	<i>Spies 3903</i>	5	WESTERN CAPE.—3418 (Simonstown): Redhill, (–AB)
	<i>Spies 4425</i>	5	WESTERN CAPE.—3318 (Cape Town): Bothmaskloof, (–BC)
	<i>Spies 4641</i>	5	WESTERN CAPE.—3420 (Bredasdorp): 4 km N of De Hoop Nature Reserve, (–AD)
<i>Catapodium rigidum</i>	<i>Davidse 33794</i>	7	WESTERN CAPE.—3420 (Bredasdorp): 20 km from Bredasdorp to Spitskop, (–CA)
	<i>Spies 3451</i>	14	WESTERN CAPE.—3420 (Bredasdorp): 6 km from Ouplaas to De Hoop Nature Reserve, (–AD)
	<i>Spies 3854</i>	7	WESTERN CAPE.—3319 (Worcester): 1 km south of old toll house in Mitchell's Pass, (–AD)
	<i>Spies 3906</i>	7	WESTERN CAPE.—3418 (Simonstown): Redhill, (–AB)
<i>Dactylis glomerata</i>	<i>Spies 4849</i>	7	EASTERN CAPE.—3228 (Butterworth): on beach at Bonza Bay, (–CC)
<i>Festuca caprina</i>	<i>Du Plessis 14</i>	14	MPUMALANGA.—2530 (Lydenburg): 18 km from Lydenburg to Weltevreden, (–AB)
	<i>Saayman 116</i>	14	MPUMALANGA.—2530 (Lydenburg): 6 km from Dullstroom to Goede Hoop, (–AC)
<i>F. costata</i>	<i>Spies 4692</i>	14	EASTERN CAPE.—3028 (Matatiele): 47 km from Rhodes in Naudes Neck, (–CC)
<i>F. elatior</i>	<i>Spies 2497</i>	14	EASTERN CAPE.—3027 (Barkly East): Beestekraal se loop, (–DC)
<i>F. scabra</i>	<i>Saayman 51</i>	14	MPUMALANGA.—2530 (Lydenburg): 16 km from Lydenburg to Sabie, (–BA)
	<i>Saayman 99</i>	14	MPUMALANGA.—2530 (Lydenburg): 17 km from Lydenburg to Roossenekal, (–AB)
	<i>Davidse 33628, 34090</i>	14	EASTERN CAPE.—3424 (Humansdorp): 10 km from Humansdorp to Cape St Francis, (–BB)
	<i>Spies 3557</i>	7	WESTERN CAPE.—3421 (Riversdale): 25 km from Droërivier to Vermaaklikheid via Oudemuragie, (–AC)
	<i>Spies 3627</i>	14	WESTERN CAPE.—3319 (Worcester): 7 km from Villiersdorp to Franschhoek, (–CC)
	<i>Spies 3962</i>	14	EASTERN CAPE.—3127 (Lady Frere): 9 km from Dordrecht to Barkly East, (–AC)
	<i>Spies 4452</i>	14	WESTERN CAPE.—3319 (Worcester): 6 km from Franschhoek to Villiersdorp, (–CC)
<i>Hainardia cylindrica</i>	<i>Spies 3192</i>	7	WESTERN CAPE.—3318 (Cape Town): 1 km east of Mamre Road, (–BC)
<i>Lolium multiflorum</i>	<i>Spies 1986</i>	7	MPUMALANGA.—2530 (Lydenburg): 14 km from Dullstroom to Lydenburg, (–AC)
	<i>Spies 2506</i>	7	EASTERN CAPE.—3027 (Lady Grey): near Barkly East, (–DC)
	<i>Spies 2663</i>	7	FREE STATE.—2826 (Brandfort): Glen, (–CD)
	<i>Spies 3191</i>	7	WESTERN CAPE.—3318 (Cape Town): 1 km east of Mamre Road, (–BC)
	<i>Spies 4428</i>	7	WESTERN CAPE.—3319 (Worcester): 8 km from Wellington to Worcester in Bainskloof, (–CA)
<i>L. perenne</i> × <i>L. multiflorum</i>	<i>Davidse 33572</i>	7	EASTERN CAPE.—3325 (Port Elizabeth): King Neptune Beach, (–DC)
	<i>Spies 3155</i>	7	WESTERN CAPE.—3319 (Worcester): Katbakkies turn-off on road between Ceres and Citrusdal, (–AB)
<i>L. rigidum</i>	<i>Spies 3183</i>	7	WESTERN CAPE.—3217 (Vredenburg): on beach outside Cape Columbine Nature Reserve, (–DD)
	<i>Spies 3190</i>	7	WESTERN CAPE.—3318 (Cape Town): 1 km east of Mamre Road, (–BC)
<i>L. temulentum</i>	<i>Spies 3386</i>	7	WESTERN CAPE.—3017 (Hondeklipbaai): dunes at Groenrivier Mouth, (–DC)
	<i>Spies 4569</i>	7	WESTERN CAPE.—3318 (Cape Town): 7 km from Yzerfontein to Darling, (–AC)
	<i>Spies 4576</i>	7+1B	WESTERN CAPE.—3318 (Cape Town): 5 km from Langebaan to Langebaanweg, (–DC)
	<i>Spies 4595</i>	7+0–2B	WESTERN CAPE.—3320 (Montagu): 22 km from Villiersdorp to Worcester via Koppies, (–AD)
	<i>Spies 4637</i>	7	WESTERN CAPE.—3420 (Bredasdorp): De Hoop Nature Reserve, (–AD)
	<i>Spies 4722</i>	7	EASTERN CAPE.—3027 (Lady Grey): 34 km from Rhodes to Lundean's Neck, (–DD)
<i>Lolium</i> sp.	<i>Spies 5062</i>	7	FREE STATE.—2729 (Volksrust): Verkykerskop, (–CC)
<i>Parapholis incurva</i>	<i>Spies 3422</i>	7	WESTERN CAPE.—3218 (Clanwilliam): 5 km south of Elandsbaai, (–AB)
	<i>Spies 3429</i>	7	WESTERN CAPE.—3318 (Cape Town): 1 km north of Uilekraal on road between Hopefield and Darling, (–AB)
	<i>Spies 3500</i>	19	EASTERN CAPE.—3424 (Humansdorp): 10 km from Humansdorp to Cape St Francis, (–BB)
	<i>Spies 4596</i>	19	WESTERN CAPE.—3320 (Montagu): 22 km from Villiersdorp to Worcester via Koppies, (–AD)
	<i>Spies 5349</i>	21	WESTERN CAPE.—3118 (Vanrhynsdorp): 2 km from Doornbaai to Donkinbaai, (–CB)
<i>Poa annua</i>	<i>Saayman 103 & 110</i>	14	MPUMALANGA.—2530 (Lydenburg): 39 km from Lydenburg to Roossenekal, (–AA)
	<i>Spies 3193</i>	14	WESTERN CAPE.—3318 (Cape Town): 1 km east of Mamre Road, (–BC)
<i>P. binata</i>	<i>Saayman 117</i>	21	MPUMALANGA.—2530 (Lydenburg): 6 km from Goede Hoop to Dullstroom, (–AC)
	<i>Spies 4680</i>	28	EASTERN CAPE.—3028 (Matatiele): 12 km from Rhodes in Naudesnek, (–CC)
<i>P. bulbosa</i>	<i>Spies 3052</i>	21	NORTHERN CAPE.—3017 (Hondeklipbaai): 6 km from Kamieskroon in Kamiesberg Pass, (–BB)
<i>P. pratensis</i>	<i>Spies 3196</i>	21	WESTERN CAPE.—3318 (Cape Town): Afrikaanse taal memorial, (–DD)
<i>Puccinellia acroxantha</i>	<i>Spies 3126</i>	21	NORTHERN CAPE.—3119 (Calvinia): 20 km from Calvinia to Loeriesfontein, (–AB)
	<i>Spies 3134</i>	21	NORTHERN CAPE.—3220 (Sutherland): 2 km from Sutherland to Calvinia, (–BC)
<i>P. angusta</i>	<i>Spies 3187</i>	7	WESTERN CAPE.—3318 (Cape Town): Tinie Versveld Nature Reserve, (–AD)
<i>Puccinellia</i> sp.	<i>Davidse 33447</i>	7	WESTERN CAPE.—3218 (Clanwilliam): 5 km south of Bobbejaanberg Point, Elandsbaai, (–AD)
	<i>Davidse 33910</i>	7	WESTERN CAPE.—3318 (Cape Town): 10 km from Wellington to Porterville, (–DB)
	<i>Spies 3154</i>	7	WESTERN CAPE.—3319 (Worcester): Katbakkies turn-off on road between Ceres and Citrusdal, (–AB)
<i>Sphenopus divaricatus</i>	<i>Spies 3426, 3427</i>	7	WESTERN CAPE.—3218 (Clanwilliam): 5 km south of Eland's Bay, (–AB)
<i>Vulpia bromoides</i>	<i>Spies 3061</i>	21	NORTHERN CAPE.—3018 (Kamiesberg): 16 km east of Kamieskroon, (–AC)
	<i>Spies 3632</i>	7	WESTERN CAPE.—3319 (Worcester): 4 km from Franschhoek from turn-off on Villiersdorp-Grabouw road, (–CC)
<i>V. fasciculata</i>	<i>Spies 3900</i>	14	WESTERN CAPE.—3418 (Simonstown): Silvermine Nature Reserve, (–AB)
<i>V. muralis</i>	<i>Spies 3987</i>	21	EASTERN CAPE.—3027 (Lady Grey): 45 km from Barkly East to Rhodes, (–DD)
<i>V. myuros</i>	<i>Spies 3153</i>	21	WESTERN CAPE.—3319 (Worcester): Katbakkies turn-off on road between Ceres and Citrusdal, (–AB)
	<i>Spies 4936</i>	21	NORTHERN CAPE.—3018 (Kamiesberg): 21 km from Kamieskroon to Gamoep, (–AC)

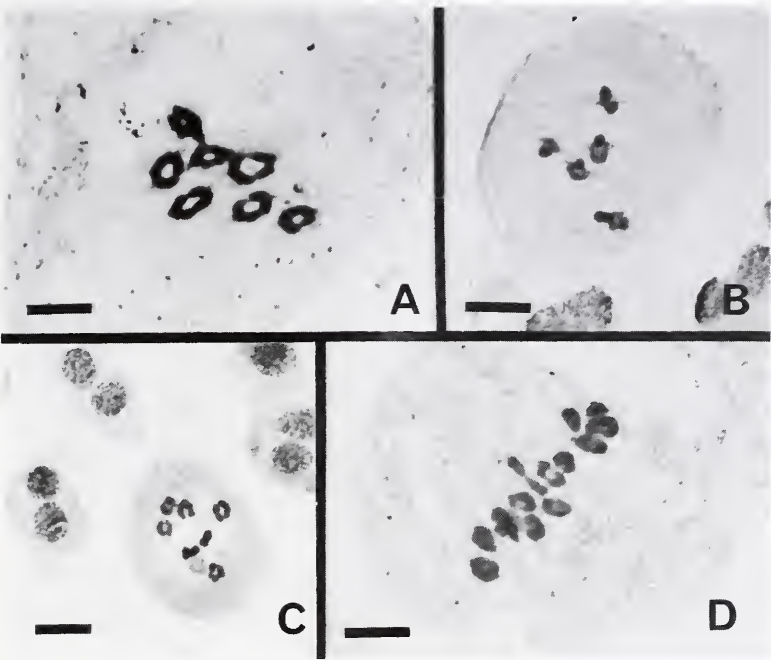


FIGURE 1.—Photomicrographs of meiotic chromosomes in the genera *Briza* and *Catapodium*. A, *B. maxima*, Spies 4420, diakinesis with 7II; B, *B. minor*, Spies 4425, diakinesis with 5II; C, *C. rigidum*, Spies 3854, diakinesis with 7II; D, *C. rigidum*, Spies 3451, metaphase I with 14II. Scale bars: 10 μ m.

ports the previous numbers recorded by various authors (Fedorov 1969; Ornduff 1967–1969; Moore 1970, 1971, 1972, 1974, 1977; Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991, 1994). To the best of our knowledge, the tetraploid number observed is a new ploidy level for *C. rigidum*. Tetraploid specimens have, however, been observed in the other *Catapodium* species. Both ploidy levels studied, formed bivalents only (Figure 1C & D) and meiosis was normal. This indicates that the tetraploid specimen may be of allopolyploid origin.

In this study the allopolyploid origin of the tetraploid *C. rigidum* specimen is supported by its genome constitution analysis, in which the observed chromosome associations concurred best with the associations expected for the 2:2 model of Kimber & Alonso (1981) (Table 2). This model indicates that two sets of genomes are present (two genomes per set) and the relative similarity between the genomes within a set is 0.5. The relative similarity between sets of genomes is expressed by an x-value that may vary between 0.5 (differences between sets are simi-

TABLE 2.—Genomic relationships in some tetraploid representatives of the tribe Poeae (Poaceae, Pooideae) in southern Africa according to the models of Kimber & Alonso (1981). The number in square brackets indicates the relative affinity of the different genomes

Species	Voucher#	4:0	3:1	2:2	2:1:1
<i>Catapodium rigidum</i>	Spies 3451	9.57	9.94 [0.5055]	2.17 [0.9995]	6.83 [0.9555]
<i>Festuca caprina</i>	Du Plessis 14	7.97	9.65 [0.9185]	0.93 [1]	3.45 [0.956]
	Saayman 116	8.69	9.87 [0.956]	0.85 [0.95]	2.65 [0.971]
<i>F. costata</i>	Spies 4692	10.56	14.35 [0.9915]	3.14 [1]	8.65 [0.9903]
<i>F. elatior</i>	Spies 2497	9.09	9.97 [1]	0.3 [1]	1.47 [0.9815]
<i>F. scabra</i>	Davidse 34090	14.33	14.48 [0.9805]	0.02 [1]	0.14 [0.95]
	Saayman 51	11.11	11.43 [0.971]	6.25 [1]	0.29 [1]
	Saayman 99	9.84	10.32 [0.926]	0.14 [1]	0.77 [0.9915]
	Spies 3627	8.92	9.79 [0.955]	0.38 [1]	1.79 [0.9805]
	Spies 3962	9.9	13.32 [1]	2.5 [1]	7.4 [0.926]
	Spies 4452	9.67	12.9 [1]	2.27 [1]	7.14 [0.955]

lar to the differences within a set, therefore the genomes may be presented in the form of AAAA) and 1 (sets differing greatly, therefore the genomes may be presented as AABB). The x-value for the tetraploid *C. rigidum* specimen is almost 1 (Table 2) and, therefore, very little to no homology exists between the two chromosome sets (genomes may be presented by AAA'A', where A differs greatly from A').

Colpodium contains three species, with *C. hedbergii* (Melderis) Tzvelev being indigenous to this country. This species was not included in this study. However, chromosome numbers of $2n = 4, 8, 14$ and 28 have been reported for the genus *Colpodium* (Ornduff 1967–1969; Moore 1970, 1971, 1972, 1974, 1977; Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991, 1994), and $2n = 8$ for *C. hedbergii* (Hedberg & Hedberg 1977). Further studies are necessary to determine the basic chromosome number of this genus and also to determine the phylogenetic development of chromosome numbers.

Cynosurus has eight species worldwide, with *C. col-oratus* Lehm. ex Nees being a very rare indigenous species and *C. echinatus* L. a naturalized species. Neither of these species was included in this study. Chromosome number reports indicate that all species studied are diploid and *C. echinatus* was included in some of those studies (Ornduff 1967–1969; Moore 1970, 1971, 1972, 1974, 1977; Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991, 1994).

Dactylis is represented in South Africa by one naturalized species (*D. glomerata* L.). The specimen of *D. glomerata* studied, was diploid (Table 1). This finding supports the various chromosome number reports of $2n = 14$ or 28 for *D. glomerata*, as well as for the genus *Dactylis* in general (Fedorov 1969; Ornduff 1967–1969; Moore 1970, 1971, 1972, 1974, 1977; Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991, 1994).

Festuca has approximately 360 species worldwide and is represented by eight indigenous species: *F. africana*

(Hack.) Clayton, *F. caprina* Nees, *F. costata* Nees, *F. dracomontana* H.P.Linder, *F. killickii* Kenn.-O'Byrne, *F. longipes* Stapf, *F. scabra* Vahl and *F. vulpioides* Steud., and one naturalized species: *F. elatior* L. (= *F. arundinacea*). Four *Festuca* species were included in this study. They were all found to be tetraploid except for one of the seven specimens of *F. scabra*, which was diploid (Table 1). In this study the tetraploid chromosome numbers ($n = 2x = 14$) were observed for *F. caprina*; this represents a new ploidy level for this species. Previous reports gave an octoploid number ($n = 4x = 28$) for this species (Spies & Du Plessis 1986a, b). This study confirms a tetraploid chromosome number ($n = 2x = 14$) for *F. costata* (De Wet 1958). The tetraploid number ($n = 2x = 14$) for *F. elatior* is in support of one of the ploidy levels previously described for this species, namely $2n = 14, 28, 42, 56$ and 70 (Fedorov 1969; Ornduff 1967–1969; Moore 1970, 1971, 1972, 1974, 1977; Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991, 1994). *Festuca longipes* was not included in this study but Hill (1965) reported a hexaploid number for this species. This is the first study to report a diploid chromosome number for *F. scabra*. The tetraploid number observed confirms the level previously reported with nonaploid and decaploid numbers (De Wet & Anderson 1956; De Wet 1958; Spies & Du Plessis 1986a, b). The chromosome numbers of four South African species of *Festuca* are still unknown, i.e. *F. africana*, *F. dracomontana*, *F. killickii* and *F. vulpioides*.

Meiosis was normal in most specimens, with only bivalents being formed (Figure 2), excepting a telophase I cell with four micronuclei in *F. costata* (Figure 2C) and a telophase II cell in one *F. scabra* specimen, Spies 3962, with a micronucleus and the possible remnants of an anaphase II bridge (Figure 2E). This low frequency of abnormalities (less than one cell in the forty cells studied per specimen), may be attributed to accidental misdivisions. The presence of only bivalents found in the tetraploid specimens of *F. caprina* (Figure 2A), *F. costata* (Figure 2B), *F. elatior* and *F. scabra* (Figure 2D), suggests that these species have allopolyploid origins.

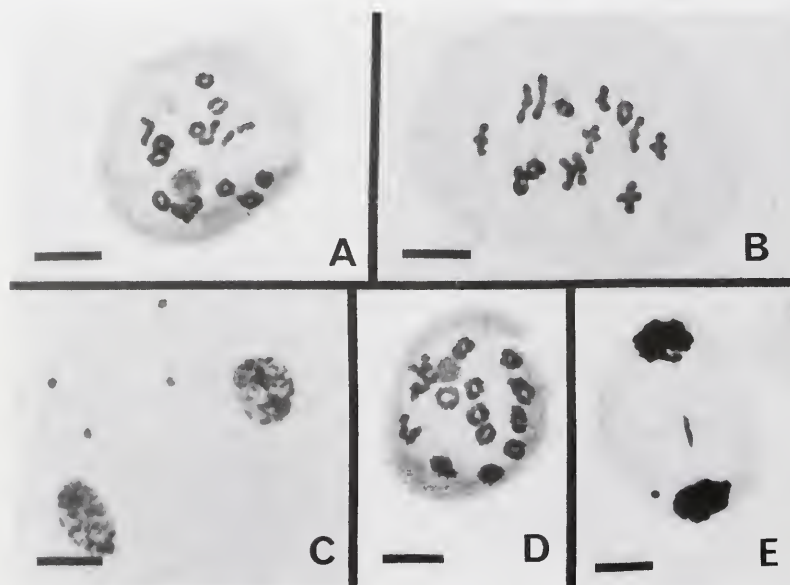


FIGURE 2.—Photomicrographs of meiotic chromosomes in the genus *Festuca*. A, *F. caprina*, Saayman 116, diakinesis with 14II. B, C, *F. costata*, Spies 4692: B, metaphase I with 14II; C, telophase I with four micronuclei. D, E, *F. scabra*: D, Saayman 99, diakinesis with 14II; E, Spies 3962, telophase II with micronucleus and possible remnant of anaphase II bridge. Scale bars: 10 µm.

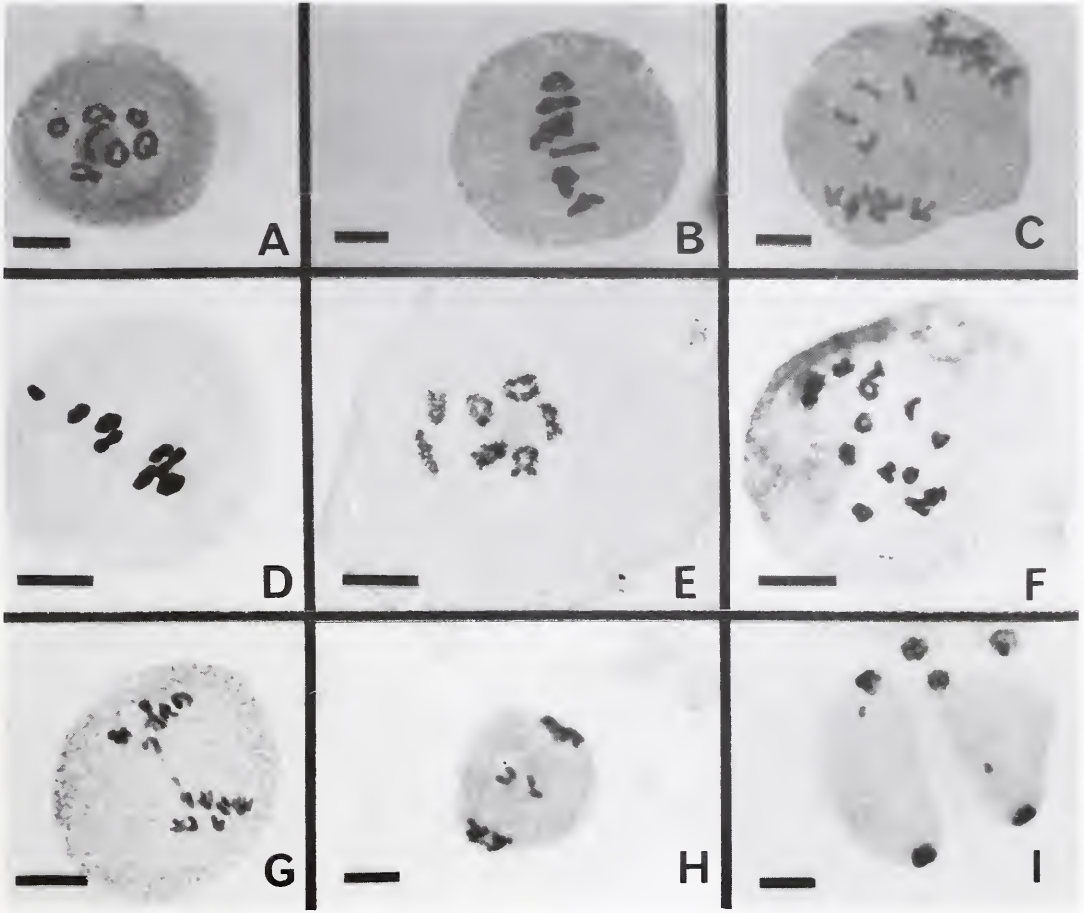


FIGURE 3.—Photomicrographs of meiotic chromosomes in the genus *Lolium*. A, *L. rigidum*, Spies 3190, diakinesis with 7II; B, *L. perenne* × *L. multiflorum*, Spies 2463, metaphase I with 7II; C, *L. multiflorum*, Spies 4428, anaphase I with 4 laggards. D–G, *L. temulentum*: D, Spies 4567, metaphase I with 7II + 1B; E, Spies 4637, diplotene with 7II; F, Spies 4637, diakinesis with 14II; G, Spies 4569, anaphase I with chromatin strand connecting two segregating chromosomes. H, I, *Lolium* sp., Spies 5062: H, anaphase II with four laggards; I, telophase II with two micronuclei. Scale bars: 10 µm.

Genome analyses of all tetraploid *Festuca* specimens indicated that, in each case, the observed chromosome associations concurred best with the expected associations for the 2:2 model (Table 2). The x -values varied from 0.95 to 1 and the analysed specimens of all four species suggest an allopolyploid origin (Table 2).

Hainardia is a monotypic genus, and *H. cylindrica* (Willd.) Greuter is naturalized in this country. We observed a diploid chromosome number of $n = x = 7$ in this species (Table 1). This number deviates from the $2n = 26$ given in the literature (Scrugli & Bocchieri 1977, mentioned in Goldblatt 1981). Further studies of this extremely rare species are necessary to determine its basic chromosome number and the possible evolutionary change from $x = 7$ to $x = 13$.

Lamarckia aurea (L.) Moench represents another monotypic naturalized genus in South Africa. No suitable material of this species could be obtained for this study. All the published chromosome numbers given agree that the species is diploid ($2n = 2x = 14$) (Fedorov 1969;

Moore 1970, 1971, 1972, 1974, 1977; Goldblatt 1988; Goldblatt & Johnson 1994).

Four species of the genus *Lolium* are naturalized in South Africa, i.e. *L. multiflorum* Lam., *L. perenne* L., *L. rigidum* Gaudin and *L. temulentum* L. All four species were studied and were all diploid (Figure 3A, B, D & E), thus confirming previous chromosome number reports (Fedorov 1969; Ornduff 1967–1969; Moore 1970, 1971, 1972, 1974, 1977; Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991, 1994). A single tetraploid cell was observed in a *L. temulentum* specimen (Figure 3F). This tetraploid cell may be attributed to cell fusion (Spies & Van Wyk 1995). A few meiotic abnormalities were observed. They include anaphase I laggards (Figure 3C), the presence of B-chromosomes (Figure 3D), an anaphase I bridge (Figure 3G), anaphase II laggards (Figure 3H) and telophase II micronuclei (Figure 3I).

The genus *Parapholis* comprises six species, but only *P. incurva* (L.) C.E.Hubb. is locally naturalized. Five specimens were included in this study (Table 1). With a

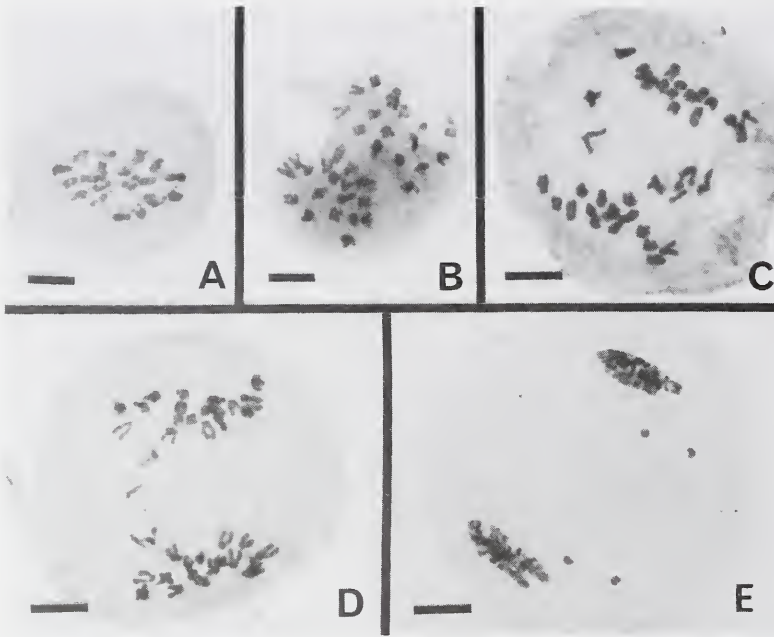


FIGURE 4.—Photomicrographs of meiotic chromosomes in *Parapholis incurva*. A, *Spies* 5349, metaphase I with 19 Π . B–E, *Spies* 4596: B, anaphase I with 18–19 segregation of chromosomes; C, anaphase I with chromosome laggards; D, anaphase I with chromatid bridge; E, telophase I with four micronuclei. Scale bars: 10 μ m.

basic chromosome number of 7, two specimens were diploid ($n = x = 7$), two aneuploid ($n = 18$ and $n = 19$) (Figure 4A & B), and one hexaploid ($n = 3x = 21$). These conflicting chromosome numbers are accentuated by the literature consulted, where $2n = 24$ (Goldblatt & Johnson 1994), 28 (Moore 1977), 36 (Fedorov 1969; Moore 1972; Goldblatt 1981), 38 (Fedorov 1969; Moore 1972; Goldblatt 1981) and 42 (Fedorov 1969) are found for *P. incurva*. Other *Parapholis* species are either diploid

($2n = 14$) (Fedorov 1969) or tetraploid ($2n = 28$) (Moore 1972). Further studies in *P. incurva* are needed to determine the evolution of chromosome numbers.

Meiosis was relatively normal and abnormalities were only observed in the aneuploid specimens (Figure 4). These abnormalities include chromosome laggards during anaphase I (Figure 4C), a chromatid bridge during anaphase I (Figure 4D) and micronuclei during telophase I (Figure 4E).

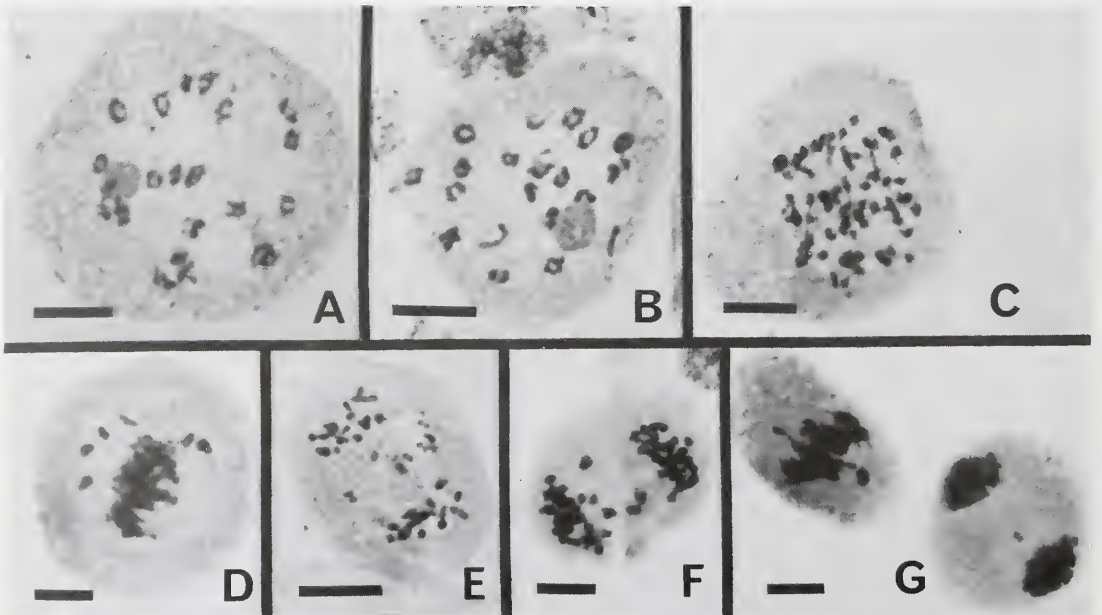


FIGURE 5.—Photomicrographs of meiotic chromosomes in the genus *Poa*. A, B, *P. binata*, *Saayman* 117, diakinesis with 21 Π . C–G, *P. pratensis*: C, *Spies* 4670, diakinesis; D, *Spies* 4670, metaphase I with several univalents; E, *Spies* 3196, anaphase I with laggards; F, *Spies* 4720, anaphase I with laggards; G, *Spies* 4720, telophase I with micronucleus. Scale bars: 10 μ m.

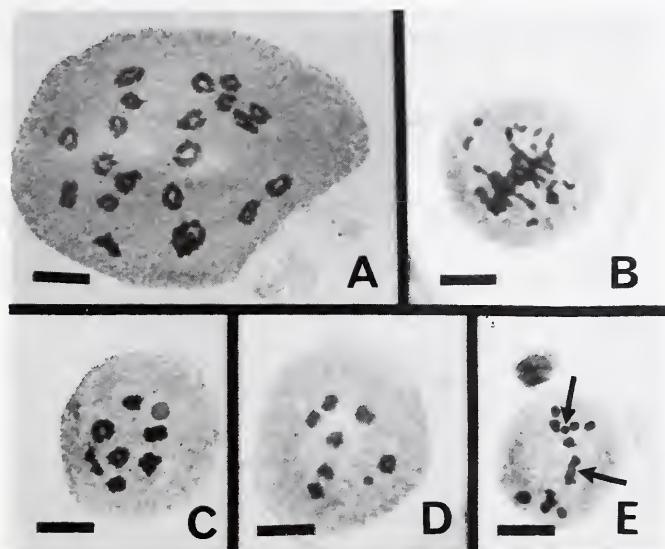


FIGURE 6.—Photomicrographs of meiotic chromosomes in the genus *Puccinellia*. A, B, *P. acroxantha*: A, *Spies* 3126, diakinesis with 21 Π ; B, *Spies* 3134, metaphase I with various univalents. C, *P. angusta*, *Spies* 3157a, diakinesis with 7 Π ; D, *Puccinellia* sp., *Spies* 3154, diakinesis with 7 Π + 1B; E, *P. angusta*, *Spies* 3157a, anaphase I with a chromosome bridge and either a B-chromosome or fragment in upper pole (see arrows). Scale bars: 10 μ m.

The largest genus in the Poeae, *Poa*, consists of approximately 500 species, with three indigenous species (*P. binata* Nees, *P. bulbosa* L. and *P. leptoclada* A.Rich.) and three naturalized species (*P. annua* L., *P. pratensis* L. and *P. trivialis* L.). Four of these species were studied. The *P. annua* specimens were tetraploid, *P. binata* had one hexaploid (Figure 5A & B) and one octoploid specimen, whereas all the *P. bulbosa* and *P. pratensis* specimens were hexaploid (Figure 5C). To the best of our knowledge, this is the first report on chromosome numbers for *P. binata*. The rest of our chromosome number reports support the previous counts made for *P. annua*, *P. bulbosa*, *P. pratensis* and *P. trivialis*.

Meiosis was abnormal in the *P. pratensis* specimen ($n = 21$). These abnormalities included numerous univalents during metaphase I (Figure 5D), chromosome lag-

gards during anaphase I (Figure 5E & F) and micronuclei during telophase I (Figure 5G).

There are ± 80 species in the genus *Puccinellia*, with three indigenous species, *P. acroxantha* C.A.Sm. & C.E.Hubb., *P. angusta* (Nees) C.A.Sm. & C.E.Hubb. and *P. fasciculata* (Torr.) C.Bicknell; and a naturalized species *P. distans* (L.) Parl. The *Puccinellia acroxantha* specimens were hexaploid (Figure 6A) and the *P. angusta* specimen was diploid (Figure 6C & D). These are thought to be the first reports on chromosome numbers for both species. A metaphase I cell with many univalents was observed (Figure 6B) in one *P. acroxantha* specimen. One B-chromosome was present in some cells of *P. angusta* (Figure 6D) and a chromosome bridge was observed in one cell of this species (Figure 6E).

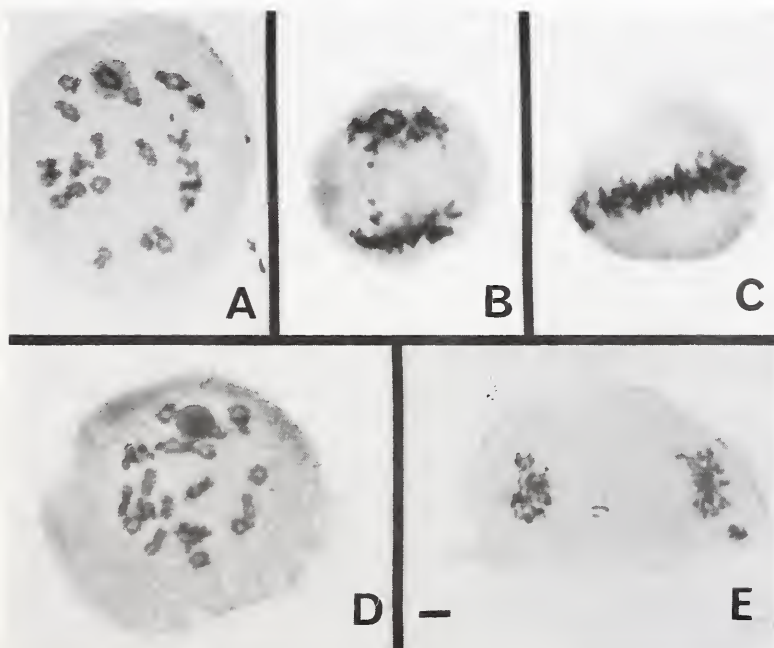


FIGURE 7.—Photomicrographs of meiotic chromosomes in the genus *Vulpia*. A, B, *V. bromoides*, *Spies* 3061: A, diakinesis with 21 Π ; B, anaphase I with chromosome laggards. C, *V. muralis*, *Spies* 3987, metaphase I. D, E, *V. myuros*, *Spies* 4936: D, diakinesis with 21 Π ; E, anaphase I with chromosome laggard. Scale bar: 10 μ m.

The genus *Sphenopus* contains two species, with only *S. divaricatus* being naturalized in South Africa. Both *S. divaricatus* specimens were diploid with $n = x = 7$. This finding contradicts the previous numbers based on six as listed in Moore 1972 & 1974 and Goldblatt 1981, and supports the $2n = 28$ listed in Moore 1972 & 1974.

Four of the 23 species of the genus *Vulpia* are naturalized in South Africa, i.e. *V. bromoides* (L.) Gray, *V. fasciculata* (Forssk.) Samp., *V. muralis* (Kunth) Nees and *V. myuros* (L.) C.C.Gmel. One *Vulpia bromoides* specimen was diploid, the other was hexaploid (Figure 7A), *V. fasciculata* was tetraploid and *V. muralis* (Figure 7C) and *V. myuros* (Figure 7D) were hexaploid. These numbers confirm the previous reported findings (Fedorov 1969; Ornduff 1967–1969; Moore 1970, 1971, 1972, 1974, 1977; Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991, 1994). Meiosis was normal in most cells with occasional chromosome laggards during anaphase I (Figure 7B & E).

This study confirms a basic chromosome number of seven for the tribe Poeae. Further studies are, however, necessary to determine the origin of the other basic chromosome numbers present in the tribe. In this regard *Briza* ($x = 5$ & 7), *Colpodium* ($x = 7$ and an aneuploid reduction series exists, or $x = 2$), *Hainardia* ($x = 7$ or 13), *Parapholis* ($x = 7$, 18 or 19) and *Sphenopus* ($x = 6$ or 7) should receive special attention.

ACKNOWLEDGEMENTS

The University of the Orange Free State and the Foundation for Research and Development are thanked for financial assistance during this study. The National Botanical Institute is thanked for providing some of the meiotic material used during this study.

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Comparative field performance of three different gas exchange systems

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Keywords: ecophysiology, gas exchange measurement, photosynthesis, transpiration

ABSTRACT

We compared portable and continuously monitoring gas exchange systems under field conditions, using *Protea glabra* Thunb. as a test species. The aim was to determine if the same patterns of gas exchange and ancillary parameters could be obtained with rather different measurement systems, and whether the same interpretation and conclusions about environmental control of gas exchange could be drawn. The following systems were compared: 1, a 'closed' portable IRGA manufactured by LI-Cor (LI-6200); 2, an 'open' portable porometer manufactured by Walz; and 3, a continuously monitoring minicuvette system with temperature control facility, also manufactured by Walz.

All three systems yielded similar diurnal curves for CO₂ uptake, although absolute flux values for the minicuvette system were lower than those obtained for the portable systems. This was likely due to stem respiration and self-shading of leaves on the shoot enclosed in the minicuvette. Differences in sampling technique between the two portable systems, primarily with regard to changes in leaf orientation, resulted in some differences in absolute values of gas fluxes and ancillary parameters such as leaf temperature and leaf to air vapour pressure difference. However, data from all three systems allowed similar interpretations to be made about the environmental dependencies of gas exchange patterns. It appears that each system has certain drawbacks associated with widely varying field conditions. A combination of portable and continuous monitoring techniques would seem to be the most powerful approach to investigating the gas exchange patterns of terrestrial plants in their natural environment.

INTRODUCTION

In the last decade, a number of advances in the simultaneous measurement of water vapour and CO₂ exchange by plant organs have been made. The present availability of several commercially produced systems provides a healthy competitive environment which is to the benefit of researchers and the quality of their science. However, the different approaches to gas exchange measurement used by gas exchange systems make them suitable for different purposes, and may also have important implications for the interpretation of results obtained when using them. In essence, no perfect all-purpose gas exchange system exists (Field *et al.* 1989). The choice of instrument for any particular task involves two fundamental trade-offs—between portability and the facility for environmental control, and between replication and resolution. Field *et al.* (1989) suggest that a combination of instruments with complementary strengths is a good solution to this dilemma. This view assumes that different gas exchange systems yield similar results, but this assumption should be tested (Reich *et al.* 1988). Apart from inadequate calibration protocol (Reich & Middelndorf 1990), concern has been expressed about the accuracy of gas flux and leaf temperature data obtained with leaf cuvettes, and the need for correction procedures (Rochette *et al.* 1990; Idso 1992). On the other hand, Monteith (1990) suggests that correction of these data is not necessary, as long as correct sampling procedures are followed.

Considering that sampling approach and technique may differ a great deal between gas exchange systems, can one

expect results yielded by them to be directly comparable? Only one published study (Winner *et al.* 1989) that we know of has addressed this important question, by comparing a closed portable photosynthesis system (LI-6200, LICOR, Lincoln, Nebraska) with an open system (ADC LCA-2, Analytical Development Corporation, Hoddesdon, England). Although the results of this study suggested that the systems gave comparable gas flux values, problems with experimental protocol prevented a conclusive result.

In this paper, we provide a direct comparison of gas exchange data obtained by three different gas exchange systems in a highly variable field environment. This is an important form of data control in a field where different research groups become more or less committed to one make or type of instrument. Our comparison is preliminary in that we do not address subtle and complex questions of cuvette design differences between instruments. We also attempt to draw attention to the advantages of combining the use of different approaches to gas exchange measurement in an ecophysiological study.

MATERIALS AND METHODS

Study site and measurement protocol

The study was carried out on the Farm Papkuilsfontein, near Nieuwoudtville, Cape Province, South Africa, in an area of natural vegetation comprising arid Fynbos and some Karoo elements. The study site was situated near the edge of an escarpment of the Bokkeveld Mountains (altitude 800 m, 33°30'S 19°05'E).

For our primary comparison, we present the results of gas exchange measurements on *Protea glabra* Thunb., an evergreen, broad-leaved, sclerophyllous shrub, made on

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MS. received: 1996-10-18.

31 January 1991 (i.e. midsummer). Measurements were made with a LICOR LI-6200 portable IRGA (LICOR, Lincoln, Nebraska, USA), a Walz CO₂/H₂O portable porometer (Walz, Effeltrich, Germany), and a continuous-monitoring minicuvette system with temperature control facility (Walz, Effeltrich, Germany). We also provide the results of a comparison between only the minicuvette system and the Walz porometer, using data collected on 29 September 1990 (spring).

In January, measurements were carried out on adult individuals which were approximately 1.5 to 2 m tall. To minimize disturbance to the individual being continuously monitored by the Walz minicuvette system for other purposes, we used the portable gas exchange systems to sample an individual of matching size and water status less than 150 m away (water potentials were measured before dawn and through the day using a pressure chamber). All gas exchange instruments were unmodified, and were used according to their instruction manuals. We attempted to synchronize sampling with the portable systems as far as possible. One leaf (that most recently fully expanded on the shoot) on each of five shoots was measured with each portable instrument at each sampling time. We returned to measure the same leaves throughout the day, except that a small number of leaves measured with the Walz porometer became detached from the plant stem; these were replaced by leaves of a comparable age and position on an adjacent stem. Towards the end of the day (after 16h00), permanently marked leaves sampled by the LI-6200 became shaded; after this occurred, well-irradiated leaves of a similar age and stem position were sampled and removed at each sampling event. Sampling of leaves with the LI-6200 was carried out with as little disturbance to the natural leaf angle as possible, although some disturbance was usually unavoidable. With the Walz porometer, the upper leaf surface was turned to face the sun after being enclosed in the cuvette, this being necessary to prevent shading of the leaf by the cuvette lid.

In September 1990, the Walz porometer was compared only with the minicuvette system. An identical procedure was followed, except that three leaves were sampled per sampling period with the Walz porometer, from a smaller shrub situated not more than 50 m from the continuously sampled individual.

Leaf areas were measured with a LI-3000 belt system, or a digitized CAD system (Summa Sketch II, programme from the Department of Plant Physiology, University of Wien, Austria).

Instrumentation

LI-Cor 6200 (LI-Cor Inc., Lincoln, Nebraska, USA)

We used this battery-powered instrument in its normal configuration, i.e. a closed system (Welles 1986). After the leaf is placed in the cuvette, air circulates between the cuvette and the gas analyser, and the CO₂ exchange rate is computed from the rate of change of CO₂ concentration due to net CO₂ uptake or loss by the leaf. Air vapour pressure can be held constant by manually adjusting a

valve which allows a portion of the circulating air to pass through a magnesium perchlorate dessicant column—in this way the effect of leaf transpiration on the vapour pressure of the enclosed air volume can be countered. Leaf temperature is measured by a chromel-constantan thermocouple which makes contact with the underside of the leaf when the hinged lid of the cuvette is closed. Air temperature in the cuvette is measured by a shielded thermistor. Relative humidity is measured by a capacitance sensor (Vaisala Humicap), which is situated beneath the radiation shield in the cuvette. The gas analyser (LI-6250) is a non-dispersive, infrared type which is tuned to the 4.26 micrometer band, providing rejection of IR absorption by gases other than CO₂. The analyser uses as a reference gas, a closed loop of air that is continuously scrubbed of CO₂. Any drift in this zero reference was checked roughly every two hours during the field work, by switching the measurement air loop through a soda lime scrubber, without a leaf in the sample cuvette. We used a standard 0.251 chamber (LI-6000-13), which is constructed of polycarbonate, and has a teflon-coated inner surface to minimize adsorption and desorption effects. The cuvette contains a small fan which minimizes boundary layer resistance. Incident photosynthetic photon flux density is measured by a LI-190S-I quantum sensor, which is mounted parallel with the sampled leaf surface.

Walz CO₂/H₂O porometer (Walz, Effeltrich, Germany)

This instrument is best operated with the aid of generator-supplied power. A 12V motor car battery may be used under field conditions, but this results in a poor IRGA temperature stabilization, and subsequent drifts in the CO₂ zero point. The instrument is normally configured as an open system (Schulze *et al.* 1982). Gas exchange rate is calculated from the difference in concentration between a reference gas line which samples ambient air, and a sample gas line which is passed through a cuvette containing the sampled leaf. Water vapour and CO₂ concentrations are measured by a BINOS I differential infrared gas analyser (Leybold Heraeus, Hanau, Germany). The zero point of the H₂O and CO₂ of the BINOS is recorded after every five measurements for later calculation correction. This is carried out by making a measurement in the normal way, but without a leaf in the cuvette. The flowrate in the measurement line is controlled by a flowmeter (Tylan, Carson, California, USA).

The sample cuvette is cylindrical (inner diameter 42 mm, height 130 mm) and has a nickel-plated inner surface. A hinged lid covered by polyethylene foil is used to seal the sampled leaf at the top of the cuvette. The cuvette has a circular radiation shield, and a fan ventilates the space between this and the cuvette to maximize heat transfer. Leaf temperature is measured by a chromel-alumel thermocouple which presses on the underside of the leaf when it is enclosed in the cuvette. Cuvette air temperature is measured by a thermistor. Cuvette humidity is measured by a capacitance sensor (Vaisala Humicap). The cuvette contains a small fan which minimizes boundary layer resistance. Incident photosynthetic photon flux density is measured by a LI-190S quantum sensor, which is mounted parallel with the sampled leaf surface.

Walz minicuvette system (Walz, Effeltrich, Germany)

This system can be operated in the field only with the aid of power supplied by at least a 0.6 kW generator. The instrument is configured as an open system, but with a continuous zero reference, obviating the requirement for removing the leaf from the sample cuvette to check the IRGA zero. The humidity of air in the sample and reference paths may be manipulated by a dewpoint controller. Differences in H₂O and CO₂ concentrations between measurement and reference paths are measured by a differential infrared gas analyser (BINOS I, Leybold Heraeus, Hanau, Germany). Two dewpoint mirrors (MTS MK1, Walz, Effeltrich, Germany) are mounted in the flowpath of the measurement gas, one measuring the dewpoint of air entering the cuvette, and the other the exiting air. This allows calculation of air vapour pressure and transpiration rate which is independent of the reading provided by the BINOS. This is especially important when high daytime transpiration rates exceed the range of the BINOS water vapour channel.

The minicuvette (GK 022) consists of two parts: an environmental control system of mainly nickel construction mounted inside a polyethylene shield, and a plexiglass leaf chamber. Chamber air temperature is controlled by Peltier elements which are thermally connected to a heat sink ventilated by a small fan. Cuvette air temperature can be set to track that of ambient air (measured by a ventilated PT100 resistance temperature sensor), or can be set to maintain a user-defined constant temperature. Under field conditions the former option is most commonly used. Chamber vapour pressure deficit can also be controlled, or set to track that of the ambient air. The instrument setup can utilize more than one sample cuvette.

The cuvette design allows a whole shoot of the target plant to be sampled in its natural position (different chamber types can be constructed which provide great flexibility in sampling). Leaf temperature is measured by a nickel-chromel thermocouple which is pressed to the underside of a representative leaf. Chamber air temperature is measured by a radiation-shielded thermistor. Photosynthetic photon flux density is measured by a LI-190S quantum sensor. A data logger stores data from relevant channels, and controls the timing of the IRGA zeroing sequence. The data can be transferred to a personal computer for further computation. The IRGA, pumps and data logging facilities are best mounted in a medium-sized vehicle (such as a minibus) for mobility, and to alleviate the harsh conditions often encountered in the field.

Calculation of gas fluxes and conductances

All gas exchange parameters were calculated after Von Caemmerer & Farquhar (1981) for all three measurement systems. All fluxes are expressed on a total leaf area basis (i.e. the total of the upper plus lower leaf surfaces), as leaves are amphistomatous in this species.

The LI-6200 and the two Walz systems differ slightly in their approach to calculating leaf conductance to water vapour. The LI-6200 software computes stomatal conductance (g_s) from leaf conductance to water vapour (g_{H_2O})

by correcting for leaf boundary layer conductance (g_b), according to the equation

$$1/g_s = 1/g_{H_2O} - 1/g_b$$

The boundary layer conductance value should be experimentally verified for different leaf shapes and sizes, and may vary according to leaf position in the cuvette. We used a nominal figure for g_b of 1.7 mol m⁻² s⁻¹, which was obtained by using a wet filter paper replica of a sampled leaf in a standard position in the cuvette. The Walz systems compute total leaf conductance to water vapour (g_{H_2O}), and do not derive stomatal conductance.

Converting g_s computed by the LI-6200 to g_{H_2O} reduced the conductance value by roughly 0.6% per 10 mmol m⁻² s⁻¹ (i.e. a g_s of 100 mmol m⁻² s⁻¹ is equal to g_{H_2O} of 94 mmol m⁻² s⁻¹), which, within the conductance range of the species used in this study, is a trivial correction in relation to other possible sources of error. Therefore, in this paper we treat g_s derived by the LI-6200 as equivalent to g_{H_2O} from the Walz instruments, as would be the situation when comparing separately published values.

RESULTS

Carbon dioxide exchange

The diurnal pattern of CO₂ exchange (Figure 1A) yielded by the three instruments was qualitatively similar, with a clear mid-morning peak, followed by a rapid decrease (less rapid for the LI-6200) towards midday, and a steady but less marked decrease towards the evening. The daily maximum CO₂ uptake rate was recorded during the same period for all systems; maximum rate yielded by the minicuvette system (3 μmol m⁻² s⁻¹) was lower than the mean recorded by the LI-6200 (3.8 μmol m⁻² s⁻¹) and the Walz porometer (4.9 μmol m⁻² s⁻¹). Data variability for the portable systems (i.e. the coefficient of variation for each sample period mean expressed as a percentage), was considerably greater for the LI-6200 (typically 37%) than for the Walz (typically 27%) during the light period. Neither portable system gave a realistic value for respiration rate at low light levels in the early morning, but the LI-6200 measured a mean respiration rate comparable to that given by the minicuvette system at the end of the day.

Integrated CO₂ uptake for the light period on the January sampling date for the Walz porometer was 120 mmol CO₂ m⁻², double that of the minicuvette system (57 mmol CO₂ m⁻²), with the value for the LI-6200 between these (99 mmol CO₂ m⁻²).

Water vapour exchange and stomatal conductance

All three systems gave qualitatively matching patterns for transpiration, and comparable maximum values (Figure 1B). However, peak transpiration was measured earliest by the Walz porometer (around 10h00) later by the minicuvette system (12h00), and latest in the day by the LI-6200 (13h00). Data variability for the two portable systems was similar (coefficient of variation around 30% of the mean for each sample time during the light period). It is likely that large transpirational water loss rates by leaves in the minicuvette system resulted in condensation in the meas-

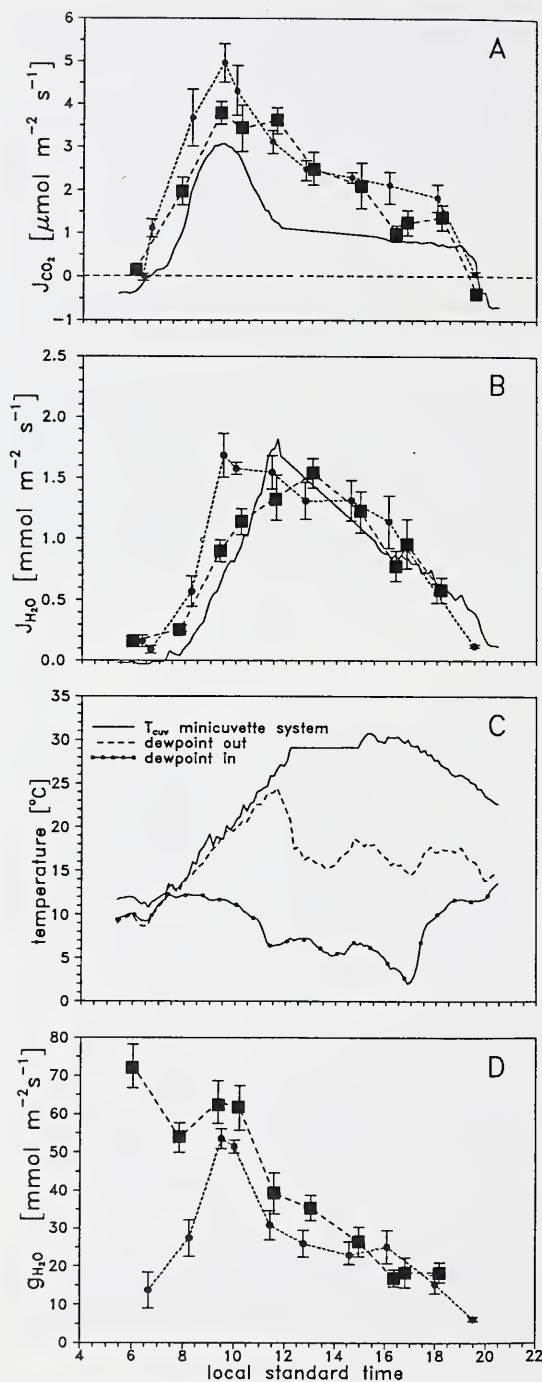


FIGURE 1.—Diurnal trends, using *Protea glabra* as test species, of parameters measured by three different gas exchange systems on 31 January 1991. A, CO₂ flux; B, transpiration rate; C, cuvette temperature and dewpoint temperatures of air entering and exiting sample cuvette on Walz minicuvette system; D, stomatal conductance for Walz and LICOR portable systems. A, B, D: Walz porometer, ●; LI-6200, ■; C, Walz minicuvette system, —; dewpoint out, ---; dewpoint in, ····. Vertical bars represent standard deviations.

using gas flowpath in the region of the cuvette. This is reflected in the parallel changes in ambient cuvette temperature and the dewpoint temperature of exiting air be-

fore 12h00 in the minicuvette system (Figure 1C), and it is unlikely that the transpiration values as measured by this instrument under these conditions are biologically meaningful.

The pattern of stomatal conductance as measured by the two portable systems, as well as the absolute values and data variability, agree well for most of the day, except for a marked divergence between the two systems before 09h00 (Figure 1D). The transpiration rates measured and conductances calculated by the LI-6200 for the last sampling period were highly variable, and sometimes negative, and are not given.

Physical parameters

Each measurement system was applied in a slightly different way in the field, and this led to some differences in measured physical parameters such as PPFD (Figure 2A). The Walz porometer measured higher values from earlier in the day than the LI-6200, due to the need to orientate the enclosed leaf towards the sun (unfortunately the Walz porometer used by us did not have the facility to provide readings greater than 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Measured leaf temperature in the Walz minicuvette system was much lower through the day than that measured by either portable system, and the Walz porometer yielded higher leaf temperatures than the LI-6200 (Figure 2B). These temperature differences led also to different leaf to air vapour pressure differences (ΔW) in each system (Figure 2C).

Secondary comparison

The comparison of transpiration rate measured by the Walz porometer and minicuvette system in September 1990 (Figure 3A) show better agreement in qualitative pattern, and give the expected lower maximum (due to lower ΔW) measured by the minicuvette system. Also, conductance patterns for these two systems were quantitatively and qualitatively comparable on that day (Figure 3B).

Summary relationships

Linear regressions fitted to plots of CO₂ exchange rate against stomatal conductance (Figure 4A, B) were significantly positive. The slopes of this relationship compared well with the Walz systems in September 1990, but the LI-6200 gave a somewhat reduced slope value than the Walz porometer in January 1991, and the lowest correlation coefficient for the regression.

Linear regressions fitted to plots of stomatal conductance against leaf to air vapour pressure difference were significantly negative (Figure 5A, B), and the slope of this relationship given by the portable instruments was comparable on both dates. The Walz minicuvette system gave by far the highest correlation coefficient for this regression, and the slope of the relationship was slightly steeper than for the portable machines.

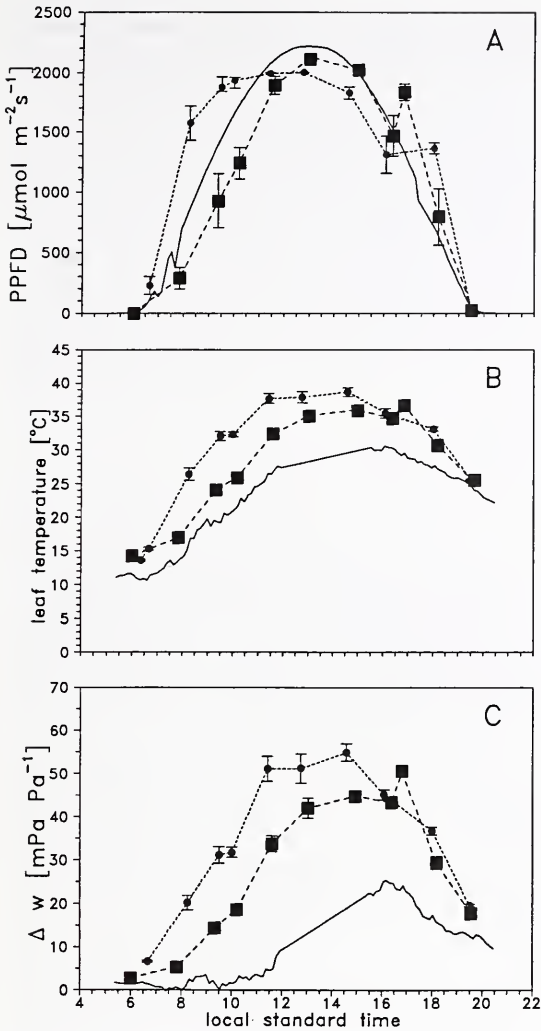


FIGURE 2.—Diurnal trends, using *Protea glabra* as test species, of physical parameters measured by three different gas exchange systems on 31 January 1991. A, photosynthetic photon flux density; B, leaf temperature; C, leaf to air vapour pressure difference. Walz porometer, \bullet ; LI-6200, \blacksquare ; Walz minicuvette system, \blacktriangle . Vertical bars represent standard deviations.

DISCUSSION

Our simultaneous use of three different gas exchange systems highlighted some heartening similarities in their data outputs. In contrast to the study of Winner *et al.* (1989), the test species used in this study had a clear diurnal pattern of water vapour and CO_2 exchange which was revealed by all three systems. However, the data also suggest some important differences between systems which may to a large extent be minimized by improvement in system design or standardization of sampling technique. The biggest difference was found between the portable machines and the Walz minicuvette system, in terms of absolute values of CO_2 and water vapour flux, and subsequently calculated conductances. This may be explained by the inclusion of a whole shoot in the minicuvette system, an approach which had three obvious implications: 1, the gas exchange of leaves with a range of ages was sampled. It has been established that young

leaves of *Protea* species tend to have lower photosynthetic rates than developing and mature leaves (Von Willert *et al.* 1989; Van der Heyden & Lewis 1990). The contribution of all leaves in the cuvette to net CO_2 and water vapour exchange is equally weighted as these fluxes are calculated on a leaf area basis. This would lead to an underestimation of these fluxes relative to those measured by the portable systems, which were used to sample only mature leaves; 2, leaves on the shoot were self-shaded to a greater or lesser extent or obliquely positioned relative to the sun's rays depending on the position of the sun (and more closely representing the real situation in the field); 3, stem material enclosed in the Walz minicuvette sample chamber would have contributed respired CO_2 .

Because sampling with the LI-6200 system involved minimum disturbance to leaf orientation, while the Walz cuvette was aimed directly at the sun for some time before taking the measurement, the expectation was that Walz values of CO_2 flux during the light period would be greater than LI-6200 values. This proved to be the case, especially at midday, when leaf orientation led to the greatest difference in sampled leaf orientation between the two portable systems. Which is the correct way to sample, or indeed, is there a correct way? It can be argued that enclosing a leaf in any sampling chamber constitutes a disturbance to the leaf environment. This is especially true of gas exchange cuvettes, which use turbulent airflow generated by an internal fan to reduce the leaf boundary layer resistance. If sampling occurs rapidly enough, it is assumed that stomata do not have time to respond to this disruption, but it is likely that this assumption is violated

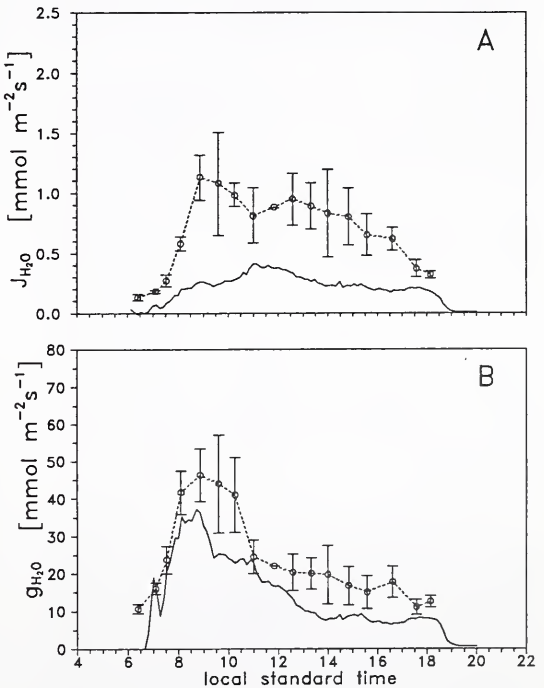


FIGURE 3.—Diurnal trends, using *Protea glabra* as test species, of parameters measured by two different gas exchange systems on 29 September 1990. A, transpiration rate; B, stomatal conductance. Walz porometer, \circ ; Walz minicuvette system, \blacksquare . Vertical bars represent standard deviations.

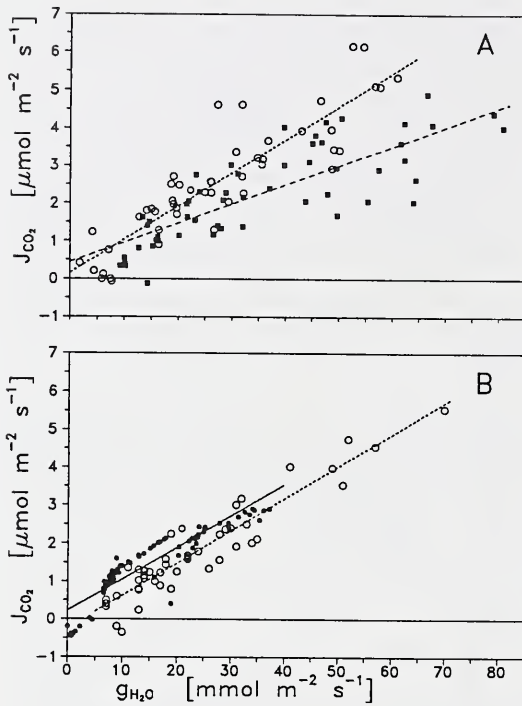


FIGURE 4.—The relationship for *Protea glabra* between stomatal conductance and CO_2 flux as measured by three different gas exchange systems. A, 31 January 1991; B, 29 September 1990. Walz porometer, \circ ; LI-6200, \blacksquare ; Walz minicuvette system, \bullet . Statistics are as follows: A, LI-6200, $r^2 = 0.65$, $df = 51$, $Y = 0.05X + 0.44$. Walz porometer, $r^2 = 0.80$, $df = 46$, $Y = 0.08X + 0.15$. B, Walz porometer, $r^2 = 0.88$, $df = 45$, $Y = 0.08X - 0.22$. Walz minicuvette system, $r^2 = 0.82$, $df = 90$, $Y = 0.08X + 0.24$.

under certain circumstances, and is species-specific. The energy balance of a leaf is also altered after being enclosed in a cuvette, but this is also assumed to have limited immediate effect on leaf function during sampling. McDermitt (1990) provides a brief summary of important considerations in this regard. Changes in leaf orientation during sampling constitute a disruption to the function of the leaf which may have immediate or delayed impacts on leaf energy balance, stomatal movements and the velocity of leaf photo- and biochemical reactions. Leaf photochemical reactions may be rapid in response to changes in light energy, but stomatal responses tend to be rather slower (Gross & Chabot 1979). If leaf orientation is to be altered for a sample, it seems prudent to establish first the rapidity of stomatal and biochemical changes in the species under study.

By changing sampled leaf orientation it is possible to control, to some extent, the PPFD incident on a sampled leaf surface using a portable system. This can be a useful technique, for example, for standardizing light conditions for different samples. In this study, the effect of standardizing light conditions (i.e. by aiming the leaf directly at the sun), using the Walz porometer, appeared to result in less noisy data, as can be seen in the correlation coefficients for the relationship between $g_{\text{H}_2\text{O}}$ and A for the portable instruments. This method could shortcut more comprehensive but time-consuming sampling strategies

for portable systems such as stratifying sampling according to leaf orientation or angle classes, but depends on knowledge of the rapidity of the physiological response.

Gas flux values obtained with a continuous monitoring system, such as the minicuvette system, may be the most accurate means of estimating diurnal carbon and water budgets, but the technique is limited by low potential for replication. Certainly, this type of system offers a level of data resolution which may improve interpretation of the effects of changing environmental conditions on gas exchange processes. This can be seen clearly in the relationship between ΔW and $g_{\text{H}_2\text{O}}$, which reveals a remarkably close relationship between these parameters that is masked by considerable variability in the data from the portable systems.

Technical limitations

Each system we used revealed shortcomings in the widely varying field environment. For the minicuvette system, the main problem seemed to be adsorption and desorption processes, especially under conditions of high air dew point temperature (i.e. in the morning on the January sampling date). The problem was not apparent on the September sampling date, when relative humidity was relatively low during the morning.

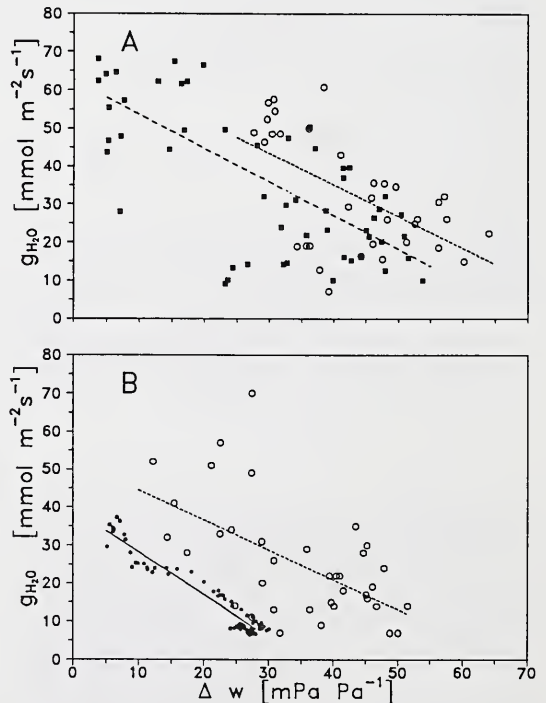


FIGURE 5.—The relationship for *Protea glabra* between leaf to air vapour pressure difference and stomatal conductance as measured by three different gas exchange systems. A, 31 January 1991; B, 29 September 1990. Walz porometer, \circ ; LI-6200, \blacksquare ; Walz minicuvette system, \bullet . Statistics are as follows: A, LI-6200, $r^2 = 0.47$, $df = 53$, $Y = -0.88X + 62.43$. Walz porometer, $r^2 = 0.32$, $df = 32$, $Y = -0.83X + 68.48$. B, Walz porometer, $r^2 = 0.33$, $df = 36$, $Y = -0.79X + 52.32$. Walz minicuvette system, $r^2 = 0.93$, $df = 68$, $Y = -1.12X + 39.38$.

Accurate measurement of water vapour concentration in the sample cuvette appeared to be a major problem for the LI-6200 early and late in the day, when humidity was high. The LI-6200 relies on an accurate measurement of this parameter for calculating transpiration rate and hence stomatal conductance. It is well documented that the accuracy of the Vaisala Humicap sensor is strongly affected above about 80% relative humidity (McDermitt 1990), and that fairly small errors in humidity measurement can lead to large errors in conductance when ambient humidity is either very low or very high (Welles 1986; McDermitt 1990); this may explain the deviation of conductance values between the portable systems early in the morning and at the end of the light period. However, the Vaisala Humicap is relatively robust within the effective range (10%–80%, McDermitt 1990), as is clear from the similarity between measurements of water vapour flux between this system and the Walz porometer through the day. The combination CO₂/H₂O IRGA used by the Walz porometer appeared to be a superior system under high humidity conditions.

Sampling with the portable systems was plagued primarily by cuvette heating problems, which were of two types: firstly, enclosed leaves heated up rapidly during measurement, and secondly, the cuvettes themselves heated up during a sampling run. Apart from direct effects on leaf function, this affects compound parameters such as leaf to air vapour pressure difference, a parameter which is thought to be of considerable importance in stomatal movements (Aphalo & Jarvis 1991), possibly through its effect on transpiration rate (Mott & Parkhurst 1991). Schulze *et al.* (1982) suggested shading the head of portable porometers between measurements to avoid heating, yet Tyree & Wilmot (1990) showed how a shaded LICOR Li-1600 porometer cuvette rapidly reduced the temperature of irradiated sugar maple leaves, leading to considerable modification of water vapour flux and calculated conductance. Recently developed portable systems which use Peltier cooling systems to allow chamber temperature to track ambient temperature may remove this limitation. This is a positive step in reducing the intrusiveness of sampling with a portable system.

CONCLUSIONS

All sampling techniques used by us yielded equivalent results, and therefore appear to be directly comparable. However, we urge users of portable systems to describe the procedure followed when clamping cuvettes onto leaves; this will contribute to more effective assessment and cross-comparison of data.

In general, matching interpretations about complex environmental and stomatal determinants of gas exchange patterns could be made using the data obtained from all three systems, which can be seen clearly in the relationships obtained between stomatal conductance and daytime CO₂ fluxes, and between ΔW and stomatal conductance. Therefore, we concur with the suggestion of Field *et al.* (1989: 239) that the combination of a continuous monitoring technique with a well designed stratified sampling strategy using a portable system, may be the most pow-

erful way to investigate gas exchange patterns in the field. It remains to be seen whether more recently developed portable systems with peltier-cooled cuvettes will increase the effectiveness of clamp-on gas exchange systems.

ACKNOWLEDGEMENTS

The support of the Deutscher Akademischer Austauschdienst and the Deutsche Forschungsgemeinschaft is acknowledged (MV, DJvW, MS). Volkswagen of SA Ltd (Uitenhage, South Africa) supplied two vehicles. We thank Willem van Wyk, owner of Papkuilsfontein at Nieuwoudtville, for permission to work on his property, and for his helpfulness and hospitality during our stay.

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OBITUARY

LESLIE CHARLES LEACH (1909–1996)

Leslie Charles Leach (Figure 1), known to friends as Larry, was born at Southend-on-Sea in Essex, England on 18 November 1909. After leaving school he passed the entrance examination of the British Army Technical School where he completed a course in electrical technology. Serving as an Army technician, he gained wide experience in electrical engineering. He applied successfully for a post in Southern Rhodesia [now Zimbabwe] and arrived in Salisbury [now Harare] in January 1938. Here he met and married Ann (often called Nan) in 1939. In 1944 he established his own business, following the acquisition of premises on Sinoia Street in Harare. Concerning himself mainly with the supply of electrical equipment for vehicles and aircraft, he traded productively under the name of L.C. Leach.

Larry's interest in succulents started in 1950 after he had purchased a 10 acre plot near Harare, which he named 'Farview'. Initially he cultivated a variety of plants, but gradually his attention centred on succulents. Larry endeavoured to learn more about succulents than could be gleaned from available literature or expertise. Soon he began to concentrate on the systematic collection of Stapelieae, Euphorbieae and species of *Aloe*.

In 1956, after selling his business, he visited the eastern Transvaal [now Mpumalanga] and southern Mozambique to compare *Euphorbia confinalis* R.A.Dyer with closely related plants that he had studied in Zimbabwe. At that time he purchased a 25 morgen plot south of Nelspruit. Satisfied that the Zimbabwean plants were distinct from *E. confinalis*, he soon embarked on several, mainly self-financed expeditions to investigate and collect the species of the *Flora zambesiaca* area, and to see as many succulent euphorbias as possible at their type localities. After the death of his wife in 1958, following a long illness, he intensified his research efforts. The journeys encompassed most of southern Africa, including Zambia, Angola, Mozambique, South Africa and Namibia, as well as Tanzania and Kenya. He was at times accompanied by R.D.A. Bayliss, I.C. Cannell, H. Hall, A.R.A. Noel, A. Percy-Lancaster, R.O.B. Rutherford-Smith, E.A.C.L.E. Schelpe, J.A. Whellan, G. Williamson, and H. Wild. His extensive expeditions are summarized in Codd (1966), Schelpe (1969) and Gomes e Sousa (1971).

The Angola trip in 1967 was partly financed by grants from the CSIR. On this occasion he collected several new records of ferns, written up by Schelpe (1968). These collecting trips were often fraught with difficulties and dangers. Two attempts to reach Goa Island, northern Mozambique, to see *E. angularis*, failed because of an allergy to mosquito bites, which he had developed on a previous excursion. However, at the third attempt, with the assistance of the Portuguese Naval Authorities, he landed on Goa Island only to find that *E. angularis* was neither flowering nor fruiting. Three years later, he was back on Goa Island, collecting flowers and fruits. In 1962

Larry was accompanied by Schelpe to collect ferns and *Euphorbia* spp. in northern Mozambique. However, a near-fatal viral dysentery grounded the expedition for a week in Blantyre.

From 1972 to 1981, Larry worked as Honorary Botanist on the staff of Zimbabwe's National Herbarium. Here he described himself as 'probably Rhodesia's only unpaid civil servant'. Larry persuaded the Aloe, Cactus and Succulent Society of Zimbabwe to publish a taxonomic series supplementary to *Excelsa*. Four volumes, containing, among others, monographs of the Stapelieae taxa *Orbea*, *Stapelia*, *Huernia* and *Tridentea*, appeared between 1978 and 1988 with Larry as the sole author. In December 1981 he emigrated to South Africa and settled first at the Botanical Research Institute in Pretoria (Figure 2) and was then employed at the National Botanic Garden at Worcester from 1982 to 1989. Until the time of his death he was employed as Honorary Research Fellow in the Department of Botany of the University of the North. Larry passed away on 18 July 1996 at the age of 86. Sadly he could not complete the treatment of the succulent Euphorbiaceae for *Flora zambesiaca* which would have culmi-



FIGURE 1.—Leslie (Larry) Charles Leach (1909–1996).



FIGURE 2.—Larry Leach at his desk at the Botanical Research Institute, Pretoria, December 1981. Photo.: courtesy of *The Pretoria News*.

nated forty years of immensely dedicated research on Euphorbieae and Stapelieae.

In later years Larry spent 'far too much' time on nomenclatural disputes. The identity of the controversial name, *Euphorbia candelabrum* is such an example (Carter 1982, 1985, 1988; editor's notes in *The Euphorbia Journal* 4: 4 (1987); Leach 1974c, 1981a, 1985b, 1986f, 1992a). Larry presented convincing arguments that *E. candelabrum* is the correct name for an arborescent species in Angola (letters to the editor of *The Euphorbia Journal* 1987). He also fought against the apparently misapplied lectotypification of *Stapelia variegata* (Leach 1981d). Convinced that the *International Code of Botanical Nomenclature* could be improved, a number of proposals for amendment of parts of the Code were unsuccessfully submitted.

Larry was a prolific collector, often in inaccessible localities in the *Flora zambesiaca* and *Flora of southern Africa* regions with $\pm 10\,000$ personal accessions being taken up in various southern African and European herbaria, although current collecting numbers are in the region of 18 000 through the inclusion of specimens sent to him for study.

Larry discovered and described four genera and 150 species and infraspecific taxa in the Euphorbieae, Stapelieae and the genus *Aloe*. Yet his most valuable contri-



FIGURE 3.—Prof. J.N. Eloff presenting the Golden Cactus Award of the International Organization for Succulent Plant Study to Larry Leach in 1990. Photo.: courtesy of *The Pretoria News*.

bution probably was the tracking down of imperfectly known species to their type localities and establishing their correct identity. His wide interest in plants resulted in his being commemorated in the following taxa: *Aloe leachii* Reynolds, *Cheilanthes leachii* (Schelpe) Schelpe, *Crassula leachii* R.Fern., *Dombeya leachii* Wild, *Echidnopsis leachii* Lavranos, *Eulophia leachii* Greatrex ex A.V.Hall, *Huernia leachii* Lavranos, × *Orbeostemon leachii* P.V.Heath, *Leachia* Plowes, *Leachiella* Plowes and *Larryleachea* Plowes.

In 1990 Leach was the first recipient in Africa of the Golden Cactus Award of the International Organization for Succulent Plant Study based in Zürich (Figure 3). He was also honoured with the Harry Bolus Medal by the Botanical Society of South Africa in 1968 (Schelpe 1969), the Gold Medal of the Rhodesian Scientific Association in 1977 (Kimberley 1977), the Certificate of Merit of the South African Association of Botanists in 1981 and the Allen Dyer medal of the Succulent Society of Southern Africa (Anon. 1994).

Larry was elected a Fellow of the Aloe and Succulent Society of Zimbabwe in 1975 and the Cactus and Succulent Society of America in 1983 (Mitich 1983). He was a vice president of the Rhodesian Aloe & Succulent Society and the African Succulent Plant Society of England.

Various tributes to Larry Leach appeared in Gomes e Sousa (1971), Schelpe (1969), Kimberley (1988), Mitich (1983) and Downs (1996).

South African botany has profited immensely from the work of highly motivated, well-versed amateurs. Larry Leach was one of the greatest among them.

ACKNOWLEDGEMENTS

I am grateful to Dr H.F. Glen (NBI) for providing some information and pictures.

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LIST OF TAXA DESCRIBED BY L.C. LEACH

Sections and subsections of genera not included. Subsequent combinations are not indicated.

EUPHORBIACEAE

*Endadenium**Euphorbia*

albipollinifera
ambroseae
ambroseae var. *spinosa*
atrocarmesina
atrocarmesina subsp. *arborescens*
bayeri
baylissii
bougheyi
bruynsii
cannellii
carunculifera
carunculifera subsp. *subfastigiata*
congestiflora
contorta
confinalis subsp. *rhodesiaca*
cooperi N.E.Br. var. *calidicola*
cuneniensis
cuneniensis subsp. *rhizomatosa*
curocana
damarana
debilis
decidua Bally & Leach
decliviticola
dedziana
demissa
dispersa
distinctissima
dissitispina
eduardoi
ephedroides E.Mey. ex Boiss.
var. *debilis*
var. *imminuta* Leach & Williamson
exilis
fanislawei
faucicola
fortissima
fragiliramulosa
francescae
gentilis N.E.Br. subsp. *tanquana*
giessii
glandularis Leach & Williamson
gracilicaulis
grandicornis Goeb. ex N.E.Br. subsp. *ejuncta*
graniticola
griseola subsp. *mashonica*
griseola subsp. *zambiensis*
halipedicola
indurescens
ingenticapsa
inundaticola
jubata
lavrani
linearibracteata
lividiflora
lowii
luapulana
lumbricalis
malevola
malevola subsp. *bechuanica*

mira

miscella
mlanjeana
monteiri Hook. f. subsp. *ramosa*
mwiniungensis
namuskluftensis
nubigena
nubigena var. *rutilans*
oligoclada
otjipembana
papilloscapa
parviceps
pedemontana
perplexa
perplexa var. *kasamana*
persistentifolia
platyrrhiza
proballiana
pteroclada
quadrilatera
radiifera
ramulosa
richardsiae
richardsiae subsp. *robusta*
rugosiflora
schmitzii
scitula
semperflorens
sereti De Wild. subsp. *variantissima*
speciosa
subsalsa Hiern subsp. *fluvialis*
strangulata N.E.Br. subsp. *deminuens*
teixeirae
tholicola
vaalputsiana
vallis
viduiflora
virosa Willd. subsp. *arenicola*
whellanii
wildii
williamsonii

Monadenium

cannellii
torrei

Synadenium halipedicola

ALOACEAE

Aloe

andongensis Baker. var. *repens*
bicomitum
cannellii
enotata
esculenta
excelsa Berger var. *breviflora*
inamara
lepidia
luapulana
procera
scorpioides
tauri
trigontha
vallis

ASCLEPIADACEAE

Caralluma caudata N.E.Br. subsp. *rhodesiaca*

Huernia

archeri

bayeri

brevirostris N.E.Br. subsp. *baviaana*

erectiloba Leach & Lavranos

formosa

guttata (Masson) Haw. subsp. *calitzdorpensis*

hislopii Turrill subsp. *robusta* Leach & Plowes

hystrix (Hook.f.) N.E.Br. var. *parvula*

lavrani

longituba N.E.Br. subsp. *cashelensis* Leach & Plowes

occulta Leach & Plowes

pillansii N.E.Br. subsp. *echidnopsioides*

plowesii

quinta (Phillips) White & Sloane var. *blyderiverensis*

thudichumii

urceolata

verekeri Stent var. *angolensis*

verekeri Stent var. *pauciflora*

Orbea

halipedicola

halipedicola subsp. *septentrionalis*

speciosa

*Orbeopsis**Orbeanthus**Pachycymbium**Stapelia*

baylissii

erectiflora N.E.Br. var. *prostratiflora*

kougabergensis

montana

montana var. *grossa*

obducta

praetermissa

praetermissa var. *luteola*

scitula

*Stapelianthus baylissii**Trichocaulon mossamedense**Tridentea baylissii* (Leach) Leach var. *ciliata*

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Book Reviews

TREE ATLAS OF SOUTHERN AFRICA/BOOMATLAS VAN SUIDER-AFRIKA. Section/Seksie 1, compiled by FRIED & JUTTA VON BREITENBACH. 1992. *Dendrological Foundation*, P.O. Box 104, Pretoria 0001. Pp. 226. Hard cover: ISBN 0620105046, price R312.00.

....'in every way a larger than life character'. This is how Hugh Glen and Mienkie Welman describe Dr Friedrich von Breitenbach in his obituary published in *Bothalia* 25: 260–264 (1995). The scope of the many achievements of this man of global vision and unquenchable determination, enthusiasm and single-mindedness equally tended to be beyond what could or would be reasonably expected. The present work, judging by its modest title, could be assumed to be little more than a collection of distribution maps of the 1 000-odd species of trees found on the sub-continent. Yet it turns out to be conceived and designed as the standard reference work on the local tree flora—the encyclopaedia of southern African trees.

The first step towards realization of this grand project was accomplished during the lifetime of Dr Fried: section 1 of a projected total of 24 sections, dealing with 1 077 tree species in 98 families and 374 genera, was published in 1992. It is dedicated to T.R. Sim, author of the first standard work on South African trees. Its 226 pages cover the 31 tree species among the ferns and gymnosperms recorded for the subcontinent.

For each species the following is provided (where relevant and/or known): National Tree number, scientific name, synonyms, common name (in up to 15 languages), description (detailed but in non-technical language), wood, taxonomy, distribution, ecology, reproduction biology, epiphytes, fungi, insects and mites, conservation, national list of Big Trees, cultivation and names (explanation of meaning/origin of common name). In addition, the following are given for each species: one or more line drawings by Jutta von Breitenbach, two or more black-and-white photographs, a colour photograph (only one species is not so illustrated in the present section), a distribution map covering half a page and depicting distribution in terms of quarter-degree squares (one-sixteenth of a one-degree square) as well as a table listing a single record, 'usually the earliest', for each quarter-degree square. For widely occurring species these lists occupy more than a page and one shudders to think what space the list of *Acacia karroo* will take up. There are detailed family and genus accounts with literature references and keys to species. No indication is given of plans to provide keys, or other aids to the identification of families, once the whole work has been completed. Colour photos are grouped together in the relevant genus account but are not specifically referred to in the text.

The book is well bound in a hard cover and is provided with a white dust cover with green print displaying title and contents, as well as the globally significant logo of the Dendrological Foundation: *arborum silvarumque conservatio salus mundi est*—the conservation of trees and forests is/will lead to the prosperity/happiness/welfare/salvation/redemption (the German word 'Heil', and similarly, the Afrikaans 'heil', say it much more succinctly) of the earth/mankind. The book, in A4 format, was produced with the aid of DTP, with English text in the left-hand column and Afrikaans on the right. Use of paper and general layout must be described as lavish, especially in view of the vast volume of the subject matter still to be dealt with and the high price of the first section. The maps could be reduced in size and produced with the aid of the MAPFIT computer program (available from the National Botanical Institute, Pretoria), the tables of distribution records much condensed, if not omitted or relegated to an appendix, the number of illustrations decreased and the layout of the work redesigned without loss of information and, if expertly handled, without detracting from the appearance of the work.

At a price of R312.00 (likely to be higher for future sections) one feels that the market of the work is largely restricted to institutions, to the most enthusiastic dendro-friends and to book collectors. But the purchaser can be assured that he acquires a work packed with thoroughly researched, comprehensive information on the dendroflora of the sub-

continent. If the project can be brought to a successful conclusion it should indeed constitute the standard encyclopaedia of southern African trees. We wish Jutta and her collaborators the resources, of various kind, the energy and the time to bring this grand project to fruition.

O.A. LEISTNER

TROPICAL ALPINE ENVIRONMENTS—PLANT FORM AND FUNCTION, edited by P.E. RUNDELL, A.P. SMITH and F.C. MEINZER. 1994. *Cambridge University Press*, The Edinburgh Building, Cambridge CB2 2RU, UK. pp 376. Price, hard cover: £65.00, \$100.00. ISBN 0-521-42089-X.

The tropic-alpine environments, with winter every night and summer every day, are radically different climatically from any other environment on our beloved, but abused planet. This appears to have resulted in some rather peculiar plant growth forms, which imply intriguing ecophysiological relationships, and consequently has excited scientific interest. The isolated occurrence of these habitats on four widely scattered land masses: Hawaii (rather marginally), South America, Africa and New Guinea, effectively provides four replicates of the natural climatic experiment.

The book aims explicitly to promote our understanding of the plant form and function in the tropic-alpine regions. It is therefore not a descriptive account, and there is little attempt at a complete regional cover (there is only a single paper on work in the New Guinean alpine region), or even a complete cover of the diversity of growth forms. The tropic-alpine setting is almost incidental to the central issue of the relationships between form and function in a peculiar environment.

The first chapters in the volume describe the tropic-alpine environments. Alan Smith's excellent review of the tropic-alpine systems constitutes a most readable chapter that stimulates a strong desire to travel to these wonderful mountains. This is followed by a rather dry chapter on the climates, full of useful information. The remaining 18 chapters fall into two groups: the first deals with general problems and adaptations (drought, temperature, anatomy), and the second constitutes reports of case studies of individual tropic-alpine taxa: *Polylepis*, *Isoetes*, *Senecio*, *Espeletia*, giant *Lobelia*, *Argyroxiphium*. These cover a range of ecophysiological subjects, as well as a few studies of herbivory, and two papers on reproductive biology. There is a single chapter on the tropic-alpine region of New Guinea: clearly this area needs more attention, especially if there is to be an attempt at arguing for convergence.

The main problems are thermoregulation and diurnal drought. Meinzer *et al.* indicate how *Espeletia* species may control minimum temperatures through a combination of growth form variation and leaf anatomy and morphology by comparing species from different altitudes, and correlating morphological and anatomical differences with altitudinal-climatic differences. In a second chapter they also deal with the drought issue, again using *Espeletia*, showing that a mechanism of major importance is capacitance, whereby plants store water to deal with a large transpiration load in the early morning, when ground temperatures may be below freezing. This is in agreement with Hedberg's findings on the *Dendrosenecio* species in Africa. However, Beck shows that the process is more complex, and that many plant tissues in *Dendrosenecio* are freeze-tolerant. He suggests that variables linked to freezing might be more important in regulating species distribution patterns.

Goldstein *et al.* show that *Polylepis* deals with its environment by a complex combination of 'adaptations' (implying morphology or anatomy that differs from the common or general situation), allowing the plants to utilize the early morning sun for photosynthesis, and to deal with low night temperatures. It does not store water as the giant rosette plants do, but tends to occupy more protected microsites.

Draba also has a diversity of survival mechanisms. Some species, like *D. chionochoila*, store enough water to transpire in the morning sun while the ground is still frozen, whereas other species, like *D. bellardii*, do not have this storage and are restricted to microsites where soil temperatures do not drop below zero. This paper is based on a comparison between the more buffered rocky habitats and the open páramo habitats.

Keeley *et al.* indulge in the bizarre when they document the extent to which tropic-alpine species of *Isoetes* derive their carbon from sediments, rather than from atmospheric CO₂. These species also completely lack stomata, and have a CAM photosynthetic pathway capable of functioning at or near freezing.

Miller investigated the role of pubescence in the inflorescences of *Puya*, and in a series of careful comparative and experimental studies shows that (a) the pubescence kept the flowers warmer and (b) warmer flowers set more seed. This is in contrast to the situation of leaf pubescence, which appears also to be related to increasing reflectance.

In one of the two papers on reproductive biology of tropic-alpine plants, Berry and Calvo document a gradual shift from bees to hummingbirds and anemophily with increasing altitude. Anemophily tends to be associated with some degree of mast-flowering. Hybridization also appears to be quite common, and Berry and Calvo suggest that habitat specificity may maintain species integrity, rather than breeding barriers. Smith & Young demonstrate many similarities in the reproductive biology between African *Dendrosenecio* and South American *Espeletia* species, including a seedling recruitment system that appears to have two 'hurdles': the first massive bout of mortality occurs during the seedling's first dry season, and the second is the failure of the seedlings to become caulescent in the presence of adults (is this a peculiar form of chemical control?). Plants tend to take decades to become reproductive.

Forty year's worth of data show that the ranges of the two giant *Lobelia* species in the Teleki Valley of Mt Kenya have undergone some dramatic changes, and Young, presenting these data, argues that occasional extreme events may have profound effects on the demography of these large plants. The fate of the giant *Lobelia* and *Dendrosenecio* on Mt Kenya is also strongly influenced by the patterns of hyrax predation: this is elegantly demonstrated by Young and Smith. This susceptibility to extreme events reminds us of the Karoo.

This book is an excellent survey of the current understanding of the ecophysiology of tropic-alpine plants. These bizarre plants provide a type of null hypothesis against which other, more typical, growth forms can be compared. I have a number of quibbles, which are with the approach, rather than the content.

A sad phenomenon is the absence of any systematic-evolutionary analysis of the evolution and origins of these weird floras. There are frequent references to the evolutionary background of the floras, yet no attempt is made to trace their origins and the route by which they acquired these amazing adaptations. The advances made in this direction by the work on the evolution of heterostyly are not utilized here. The book is very much in the non-evolutionary mould of old ecophysiological studies, and shows no signs of the new biology yet. This means that the route by which these weird and wonderful adaptations were attained is not traced.

The adaptive nature of some of the structures is not always evident from the papers. Correlation of structure and environmental variables is not a sound methodology. Much more convincing are the papers that report the results of experimental manipulations. It is very evident from this book that the study of tropic-alpine ecophysiology is still at an early stage. Different plants appear to show different methods of dealing with the same problems. Many of the presumed adaptations have not been tested rigorously, and there has been rather little experimental work.

Striking is the lack of work by indigenous African botanists. Considering the proximity of Mt Kenya to Nairobi, with its four universities and a large herbarium, this is a sad indictment, which strongly underlines the need for capacity building on our fabulous continent, especially since the pioneering work on tropic-alpine environments was done by Hedberg in Africa.

Tropic-alpine environments are often inaccessible, and evoke rather romantic images, like 'The mountains of the Moon', the Andean Páramo, and Mt Wilhelm in Papua New Guinea, which appeal to both scientists and the general public. Few people have worked in all four areas, and this is the first book that brings together diverse papers from all of them.

It is therefore essential reading for anybody interested in the tropic-alpine flora. Many of the papers are reviews by scientists who had previously published several papers on their research, and as such it is a timely book, providing an overview of the fascinating adaptations of tropic-alpine plants.

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BIODIVERSITY AND CONSERVATION OF NEOTROPICAL MONTANE FORESTS, edited by S.P. CHURCHILL, H. BALSLEV, E. FORERO & L. LUTEYN. 1995. *The New York Botanical Garden*, Bronx, New York 10458-5126, USA. Pp xiv + 702. Price, hard cover: \$85.00. ISBN 0-89327-400-3.

The New York Botanical Gardens hosted a symposium in June 1993 at which the 52 papers published in this book were presented. The authors are all intimately involved with the montane regions of the Neotropics in a variety of ways. The ecosystems in focus: the montane forests of the Neotropics, are under severe pressure and this is amply spelled out in this volume. In terms of research, emphasis has generally been placed on biodiversity and conservation of the lowland rainforests, whereas the montane region has been neglected. Large areas of mountain forests have been destroyed, resulting in dramatic fragmentation of the montane region. This is not only regrettable because of the simple loss of biodiversity but also because the genetic base of many potentially important medicinal and crop plants is lost or eroding rapidly. These inadequacies are highlighted in the book and point to the need for much greater effort to study and conserve the biodiversity of the montane Neotropics.

The book is dedicated to the memory of two outstanding neotropical botanists, Alwyn Gentry and Linda Albert de Escobar. They were two of four biologists killed in a light plane crash on 3 August 1993 in Ecuador while involved with Conservation International's Rapid Assessment Programme. It is fitting tribute that a compendium of papers such as this should honour their memory because they were so active in promoting the cause of conservation of the tropical forests. Alwyn Gentry was particularly concerned with floristic inventory and ecological diversity of tropical forests and his paper delivered at the symposium and published posthumously, bears testimony to the energy and enthusiasm he displayed in his chosen task. Other authors are no less dedicated and a continuous thread throughout the different papers is the severe impact the activities of man have had on the floral richness of the neotropical mountains over a period of about five centuries. The most startling statistic is, that whereas approximately 12% of the Amazonian rainforests have been destroyed, about 12% is all that remains of the tropical montane ecosystems. It is predicted that the future survival or demise of tropical highland vegetation in South America will be determined during the next decade, depending on whether effective conservation measures are instated or not.

The work is divided into six sections, each with a brief editorial summary. The first section sets the scene in that it explores the vegetational history from the Cretaceous to the Holocene.

Looking at this tableau as a palaeobotanist, you ask yourself: why the extraordinary plant diversity in neotropical montane forests? And truly extraordinary it is, with around one in every five species on Earth being found there. How did this unique diversity arise? What do we know of the history of the vegetation of this small and dynamic corner of our planet's surface? And what can we learn from all this?

Our answers to all these questions are patchy and embryonic. As stated in the introduction to this volume: 'An immense potential lies ahead for the contributions that can be provided by evolutionary biologists'. Just four of 52 papers published in this admirable volume of 702 pages are devoted to the floral evolution of the Neotropics. These four papers, covering the last 130 million years or so, from the Cretaceous to the present, provide the merest glimpse at some of the most important of all possible questions.

The first two contributions focus on the broad pattern of the floral origins of this mountainous cornucopia; the second pair of papers home in on the specific picture revealed in the sediments of the high plains of Bogota (Colombia) over the past five million years. It is largely through

the study of the fossil pollen record that the outline of the vegetation history is told. Understanding the complex biogeographic processes—the webs of cause and effect—will require modelling the myriad tectonic, climatic and biological factors involved in the system. Between chaos theory on the one hand and the solar constant(?) on the other, emerges, through many millions of years, the extant reality of diversity and distribution.

The palaeovegetation has suffered frequent shifts in floristic composition. The Andean forests were subject to considerable change, as shown particularly clearly for the past five million years—the interval during which man was evolving from ape in Africa. Mountain building has been episodic over the 130 million years discussed: with the centre of Andean uplift shifting from south to north and west to east. The southern Andes first arose around 100 million years back, whilst the history of the northern stretch of the chain is confined to the latter half of this period. The breakup of Gondwana and the shifting of continental plates has played a critical role: 'considerable interchange [of floras] was possible between South America and Antarctica until the early Tertiary, between South America and Africa until the mid-Cretaceous, and between South America and Meso- and North America during the Late Tertiary'. Both mountain building and continental drift dramatically affect climatic patterns. Environmental change drives evolution, brings extinction and diversification.

The incredible floral richness of the tropical northern Andes comprises many immigrants from both north and south as well as many families (17 of 40 with a known fossil record) that are centred there. The mountainous terrain is both refugium for immigrants and centre of diversification and radiation. The four papers reviewed have provided a fine and stimulating glimpse—the merest glimpse—at the floral history leading to this richness. There remains much to be learned why the Neotropics are so very much richer than the tropics of Africa and southeast Asia. Knowledge and understanding usually lead to love and devotion. This volume and these papers must surely shift our global will closer to preserving such a wonderful focal point of diversity within the biosphere and to our reaping its full benefits.

The second section of the book documents a series of studies concerning the inventory of the remarkable biological diversity. It includes 17 papers, only one of which deals with birds rather than plants. These papers cover a wide range of topics pertaining to the common goal of describing the patterns of species abundance and diversity as well as the structure of the plant communities in question. Useful information about patterns of endemism is also provided; the serious student of diversity would do well to pay attention to these papers; they provide a good source for comparison with other species-rich ecosystems in the world.

It may come as a surprise to some to find a whole section (section three) on the taxonomic diversity of cryptogamic plants. However, the extraordinary high diversity of these plants in the montane forests of the Neotropics, and the important ecological role they play in montane ecosystems, fully warrant such an inclusion. The first two papers describe diversity in selected genera of Agaricales (fungi) in *Quercus* forests (Mueller & Halling), and in lichens of the Colombian montane forests (Sipman). Although the neotropical fungi, and to a lesser extent lichens, are very incompletely known, the studies show that the potential diversity is high. An analysis of distribution patterns in selected groups of fungi reveals great potential endemism, while almost half of the lichens studied have a wide distribution throughout the tropics.

Bryophytes are better known and diversity for the tropical Andes is exceedingly high, estimated at 1 500–1 700 species distributed among 343 genera and 75 families for mosses (Churchill, Griffin & Lewis), and 800–900 species in 135 genera and 42 families for liverworts (Gradstein). The Andes may be four times as rich in liverworts, and eight times as rich in mosses as the surrounding tropical lowland areas, and the highest species diversity is in the upper montane forest, roughly between 2 500 and 3 300 m. The reason for this high diversity is thought to be topographic relief which provides favourable habitats and climatic conditions for bryophytes. This section gives a good overview of cryptogamic plant diversity in the

montane Neotropics and emphasizes the need to accelerate exploration and taxonomic revision in this fascinating group of plants.

The amazing taxonomic diversity of the Neotropics is well described in the fourth section. One paper deals with ferns, one with the Lycopodiaceae and the remaining 13 with flowering plants in a variety of families: Theaceae, Bonnetiaceae, Symplocaceae, Rosaceae, Onagraceae, Araliaceae, Asclepiadaceae, Rubiaceae, Asteraceae, Arecaceae, Poaceae (Bambuseae) and Heliconiaceae. The editorial commentary on this section particularly highlights the plight of plant systematics in the Neotropics, where it is estimated that it will take almost another 500 years to complete the taxonomic treatment of flowering plants in the *Flora neotropica*. It is clear that among plants many unknown species, perhaps some unknown genera and even some unknown families, may become extinct before even being discovered. This potentially great loss underlies the plaintive cry to train and encourage more young taxonomists and comparative biologists who could change this negative condition and foster knowledge of tropical biology and more particularly of the tropical highland flora.

The fifth section concerns the human impact and utilization of the montane environments. Disturbance of the montane ecosystems goes a long way back in history. However, the human need for physiological stimulants (drugs!) in various forms has produced the modern ever-increasing demand for such substances as caffeine, cocaine and morphine. Illegal opium plantations cover 20 000 ha in Colombia and coca cultivation results in the annual destruction of 1 000–2 000 ha of forest. In Colombia, what was once a major centre of plant diversity in the 900–2 000 m elevation zone, is the 'coffee zone'. Add to this the global desire for hardwoods, and the result is a tragic tale of rapid destruction of montane forests, particularly in Colombia, Bolivia and Ecuador. Only a decreased demand for habit-forming substances in the developed world will reduce the continued transformation of montane forests.

The final section appropriately starts with a paper by Thomas van der Hammen entitled 'Global change, biodiversity, and conservation of neotropical montane forests'. At a time when global changes are occurring in climate, geology and sociology, it is fitting that a paper such as this succinctly focuses on the response by both plants and man to these changes. Using the example of the destruction of Andean montane forests, suggestions are made as to what should be done to conserve what little is left after the historical depredations of man and the impact of future far-reaching changes of global change. The lessons learned apply globally and it is up to us to recognize the warning signs and respond positively in order to stem the tide of global degradation and attrition of biodiversity.

Ethnobotany is of common concern at a global scale and it is true that in many places many useful plants that are known and many plants that are potentially useful have been lost through habitat transformation and overexploitation. This is true in Africa, Asia and no less in South America. The paper by AnneMarie Sørensen and Inge Schjellerup, shows clearly how dependent the peasant community of Chachapoyas people in the district of Chuquibamba, is on natural products from the montane forests. The prognosis is not good—as the forest disappears so too do the natural resources upon which the peasants depend. The potential pointers to valuable products for modern medicine and improved food crops can also be lost in this process.

The main aim of this book is to encourage the conservation of the neotropical montane region. It is well edited and admirably succeeds in not only introducing the Neotropics to the uninitiated but also in providing a wealth of information about the region. It has a useful index even though the scientific names are not included. The book heightens the awareness of the need for concerted global effort and responsibility if there is to be any hope of survival for the neotropical vegetation with its great diversity.

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May 1997

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ISSN 0006 8241

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